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COMPARATIVE ANATOMY

OF

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DR. ROBERT WIEDERSHEIM 1848 –

PROFESSOR OF ANATOMY, AND DIRECTOR OF THE INSTITUTE OF HUMAN AND COMPARATIVE ANATOMY
IN THE UNIVERSITY OF FREIBURG-IN-BADEN

BY

W. N. PARKER, PH.D.

PROFESSOR OF ZOOLOGY AT THE UNIVERSITY COLLEGE OF SOUTH WALES AND MONMOUTHSHIRE
IN THE UNIVERSITY OF WALES

THIRD EDITION

(FOUNDED ON THE SIXTH GERMAN EDITION)

WITH THREE HUNDRED AND SEVENTY-TWO FIGURES
AND A BIBLIOGRAPHY

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PREFACE

THE developmental history of this book has been somewhat complicated. The first German edition appeared in 1882, under the title of *Lehrbuch der vergleichende Anatomie der Wirbeltiere*, and a second edition followed in 1886. In 1884, a short *Grundriss* was published, which, after passing through four editions and gradually increasing in size, replaced the Lehrbuch under the title of *Vergleichende Anatomie der Wirbeltiere*, in 1902. A further edition appeared in 1906, and this was followed by a shorter *Einführung* in 1907: the latter was written to meet the requirements of beginners, and it contains no bibliography.

The first and second English editions (1886 and 1897) were based respectively on the first and third editions of the *Grundriss*, and considerable modifications in detail were introduced. The present (third) edition, which has been almost entirely re-written, was prepared from the German editions of 1906 and 1907, and I am much indebted to Professor Wiedersheim for allowing me to make such alterations as seemed desirable in the interests of English students, and for the pleasure of his collaboration last summer, when I had the advantage of discussing various points with him personally.

The general plan of the original has been retained throughout, but I found it advisable to extend some portions and to abridge others, besides making various minor modifications.

After re-editing by Professor Wiedersheim, the bibliography given in the German original is inserted entire, except that the titles and references have been abbreviated and slight rearrangements made in order to save space: I have also ventured to introduce a few additions. Though rather extensive for a work of the kind, the list must not be regarded as anything approaching a complete one of the more important papers relating to Vertebrate Comparative Anatomy; but I trust that such a list of references in an easily accessible form will be found useful to advanced students.

My thanks are due to Mr. T. H. Burlend, Demonstrator and Assistant Lecturer in Zoology at this College, for preparing the index.

W. N. PARKER.

UNIVERSITY COLLEGE, CARDIFF,
August, 1907.

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ERRATA

PAGE	
5	5th line from bottom, *for* "walls," *read* "wall."
13	Fig. 11, *insert* "gonad (ovary)" *below* "kidney."
33	,, 25, *for* "*N* and *G* nerves," *read* "*N*, nerves ; *G*, blood-vessels."
40	8th line from top, *for* "disappear," *read* "disappears."
40	11th ,, ,, *for* "ossifications," *read* "ossification."
53	Fig. 42, transpose *A* and *B*.
72	Line 6 from bottom, *delete* "the first" and "cervical."
73	,, 10 ,, *for* "are," *read* "is."
73	,, 3 ,, *for* "proximal," *read* "anterior."
73	,, 2 ,, *for* "distal," *read* "posterior."
92	Fig. 69, *insert* "*O*" before "orbital ring," and "*sympl.*, symplectic."
96	,, 71, ,, "*K*, external gills."
112	3rd line from top, *for* "system," *read* "septum."
119	Fig. 86, *for* "condyles," *read* "condyle."
145	10th line from bottom, *delete* "B."
151	4th ,, top, *for* "show," *read* "shows."
155	18th ,, ,, *for* "stright," *read* "straight."
164	Fig. 129, *for* "1st," *read* "5th."
176	17th line from top, *for* "and thus effect," *read* "thus effecting."
298	Fig. 218A, *for* "*Pp*;" *read* "*Pb*."
304	,, 223, *for* "vestibula," *read* "vestibuli."
315	3rd line from top, *for* "cartilaginious," *read* "cartilaginous."
340	Fig. 250B, *for* "tendrinous," *read* "tendinous."
438	20th line from bottom, *for* "Phalcolarctos," *read* "Phascolarctos."
445	6th and 7th lines from bottom, *for* "parosphoron," *read* "paroophoron."
450	13th line from top, *for* "epididermis," *read* "epididymis."

rudimentary or vestigial organs and parts in the adult organism which would otherwise remain totally inexplicable.

Histology is a subdivision of anatomy which concerns the *structural elements*—the building-stones of the organism, and the combination of these to form **tissues**. Various combinations of the tissues give rise to **organs**, and the organs, again, combine to form **systems of organs**.

The structural elements consist primarily of **cells** and secondarily of cells and *fibres* often enclosed in an intercellular substance or *matrix*; and the different tissues may be divided into four principal groups:—

1. *Epithelium*, and its derivative, *glandular tissue*.
2. *Supporting tissue* (connective tissue, adipose tissue, cartilage, bone).
3. *Muscular tissue*.
4. *Nervous tissue*.

In accordance with the functions they perform, epithelium and supporting tissue may be described as *passive*, and muscular and nervous tissue as *active*.

By an *organ* we understand an apparatus which performs a definite function: as, for instance, the liver, which secretes bile; the gills and lungs, in which an exchange of gases is effected with the surrounding medium; and the heart, which pumps blood through the body.

The *organ-systems*, which will be treated of in order in this book, are as follows:—1. The outer covering of the body, or *integument*; 2. The *skeleton*; 3. The *muscles*, together with electric organs; 4. The *nervous system* and *sense-organs*; 5. The organs of *nutrition*, *respiration*, *circulation*, *excretion*, and *reproduction*.

The closely-allied branches of science defined above are included under the term **Morphology**, as opposed to **Physiology** which concerns the functions of organs, apart from their morphological relations. The combined results obtained from these two fields of study throw light on the organisation of animals in general—that is, on **Zoology** in its widest sense.

II. DEVELOPMENT AND STRUCTURAL PLAN OF THE VERTEBRATE BODY.

The structural elements described in the preceding section as the building-stones of the organism, *i.e.* the cells, all arise from a *single primitive cell*, the **egg-cell** or **ovum**. This forms the starting-point for the entire animal-body, and a general account of its structure and subsequent development must therefore be given here.

The ovum consists of a rounded, nucleated, protoplasmic body

(Fig. 1), consisting of the *vitellus*, in the interior of which is the *germinal vesicle*, enclosing one or more *germinal spots*: the membrane which covers the vitellus is spoken of as the *vitelline membrane*. Since the ovum corresponds to a single cell, we may speak of the vitellus as the *protoplasm* of the egg-cell, the germinal vesicle as its *nucleus*, and the germinal spot as its *nucleolus*: the vitellus, however, consists of two different substances—*protoplasm* and *deuteroplasm* (*yolk*)—in varying proportion and relative distribution in different animals.

The nucleus is enclosed by a delicate *nuclear membrane*, and is made up of two chief constituents—the *spongioplasm* or *chromatin*, and the *hyaloplasm* or *achromatin*. A small particle, the *centrosome*, is also present in the protoplasm of the cell, and takes an important part in the process of cell-division. An outer limiting membrane, corresponding to the vitelline membrane, is not an integral part of the cell, but may be differentiated from the peripheral protoplasm.

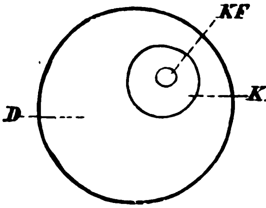


Fig. 1.—Diagram of the Ovum.

D, vitellus; *KB*, germinal vesicle; *KF*, germinal spot.

In the process of *sexual reproduction*, which occurs in all Vertebrates, the fusion with the ovum of the **sperm-cell** or **spermatozoon**, containing the generative substance of the male, is an absolute necessity for the development of the former.

Before this fusion can occur, certain changes take place in the ovum which constitute what is known as its **maturation**, the essential result of which is a reduction in mass of the chromatin in the germinal vesicle. The ovum undergoes a twice-repeated process of cell division (*karyokinesis* or *mitosis*) similar to that which occurs in tissue-cells, except that the resulting daughter-cells, in addition to the reduction in their chromatin, are of different sizes, two small evanescent *polar-cells* (Fig. 2) being successively thrown off from the larger ovum. A similar process also occurs in the development of the sperm-cell, except that there is no difference in size between the products of division. The portion of the original nucleus remaining in the ovum or sperm is then known respectively as the *female* (or *maternal*) and *male* (or *paternal*) *pronucleus*.

A sperm-cell then makes its way into the ovum, and its pronucleus unites with the female pronucleus to form the *segmentation nucleus*. This process, which is known as **impregnation** or **fertilisation**, thus consists in a material intermingling of the generative substances of both sexes, or more accurately of the sperm-nucleus and egg-nucleus. The essential cause of inheritance can thus be traced to the molecular structure of the nuclei of both male and female germinal cells. This structure is the morphological expression of the characters of the species.

After fertilisation has taken place **development** begins. The segmentation nucleus divides into two equal parts, each of which forms a new centre for the division of the **oosperm**, as it must now be called, into two halves or *blastomeres*. This division, the beginning of the process of **segmentation**, takes place by the formation of a furrow round the egg which becomes deeper and deeper until the division is complete. (Fig. 2, A).

The first stage in the process of segmentation is thus completed; the second takes place in exactly the same way, and results in a division of the oosperm into four parts; and by a similar process are formed eight, then sixteen, then thirty-two blastomeres, and so on, the cells becoming smaller and smaller, and each being provided with a nucleus. (Fig. 2, C—D). In short, out of the original oosperm a mass of cells is formed which represents the building-material of the animal body, and which, from its likeness in appearance to a mulberry, is spoken of as a **morula**.

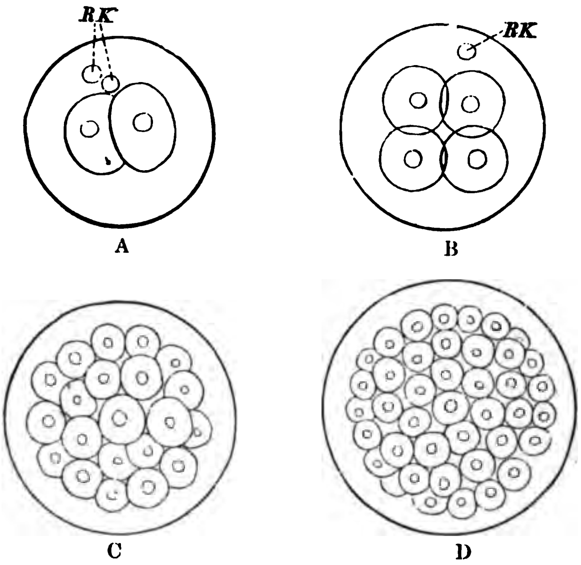


FIG. 2.—DIAGRAMS OF THE SEGMENTATION OF THE OOSPERM.

A, first stage (two segments): *RK*, polar cells. B, second stage (four segments). C, further stage. D, morula stage.

In the interior of the morula a cavity (*segmentation cavity* or *blastocœle*) filled with fluid is formed, and the morula is now spoken of as the **blastosphere** or **blastula** (Fig. 3). The peripheral cells enclosing this cavity form the **germinal membrane** or **blasto-**

derm. Consisting primarily of a single layer of cells, the blastoderm later on becomes two-layered, and then three-layered. From the relative position of these, they are spoken of respectively as the *outer*, *middle*, and *inner germinal layers*, or as **ectoderm** (*epiblast*), **mesoderm** (*mesoblast*), and **endoderm** (*hypoblast*).

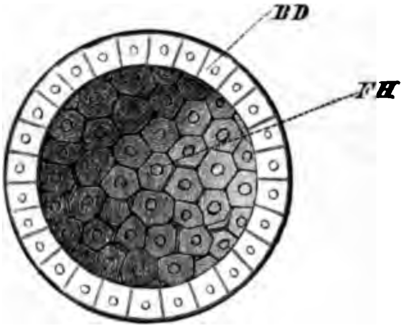


FIG. 3.—BLASTOSPHERE.

BD, blastoderm; *FH*, segmentation cavity.

The mode of distribution of the yolk-particles in the ovum, and an increase in their amount, result in certain modifications of the primitive form of segmentation as described above. Yolk is an inert substance, and its presence tends to hinder or even entirely to prevent segmentation in those parts of the ovum in which it is abundant. When the whole ovum undergoes division, the segmentation is known as *entire* or *holoblastic;* when division is restricted to part of the ovum only, the segmentation is said to be *partial* or *meroblastic*[1] (Fig. 4).

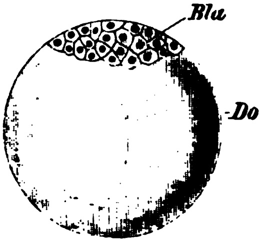


FIG. 4.—DIAGRAM OF A MEROBLASTIC OOSPERM WITH DISCOID SEGMENTATION.

Bla, blastoderm; *Do*, yolk.

The question as to the origin of the germinal layers, on account of its important signification, is one of the most burning problems in morphology, and as yet we cannot arrive at any full and satisfactory conclusion on the subject. It may, however, be stated that in all Vertebrates the blastosphere passes—or did so in earlier times—into a stage called the **gastrula**, which is retained in an unmodified form only in the lowest Vertebrate (Amphioxus, cf. p. 14). The gastrula is derived primitively from the blastula by the walls of the latter (Fig. 3) becoming pushed in or invaginated at one part, thus giving rise to a double-walled sac (Fig. 5). The outer wall then represents the ectoderm, which serves as an organ of protection and sensation, while the inner, or endoderm, encloses a central space, the primitive digestive cavity (*archenteron*). The opening of the latter to the exterior, where the two germinal layers are continuous, represents the primitive mouth or *blastopore*, which is represented to a certain extent by the *primitive streak* of higher forms.

---

[1] In holoblastic segmentation the resulting cells are approximately *equal* in the Lancelet and in Mammals (with the exception of Monotremes and some Marsupials); and *unequal* in the Cyclostomes, Sturgeon, Lepidosteus, Dipnoans, and nearly all Amphibians, the segmentation sometimes approaching the meroblastic type. In Elasmobranchs, Teleosts, Reptiles, Birds, and Monotremes the segmentation is from the first meroblastic and *discoid*, *i.e.*, restricted to the upper pole of the ovum (Fig. 4).

From the ectoderm arise the epiderm and its derivatives, the entire nervous system, the sensory cells, the lens and certain muscles of the eye, the oral and anal involutions (*stomodæum* and *proctodæum*), and the oral portion of the pituitary body attached to the brain. In an early stage the endoderm gives rise to an axial rod, the *notochord* (Figs. 6 and 7), and eventually to the epithelium of the greater part of the alimentary canal (Figs. 6 and 10) and its glands, including the thyroid, thymus, liver and pancreas, as well as to the epithelial parts of the gill-sacs and lungs.

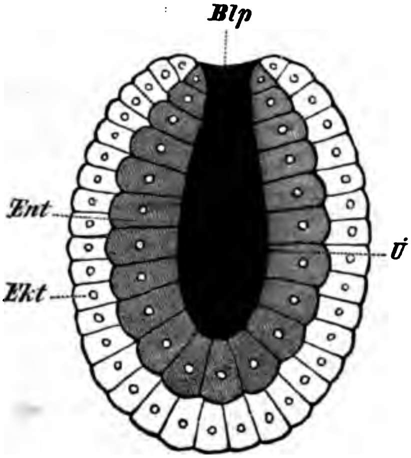


FIG. 5.—GASTRULA.

Blp, blastopore; *Ekt*, ectoderm; *Ent*, endoderm; *U*, archenteron.

Though we may look upon the ectoderm and endoderm—that is, both the primary germinal layers—as arising primitively in the manner above described, various modifications occur, depending largely on the type of segmentation, and known as *overgrowth* (*epiboly*), *delamination*, and *partial delamination*. The middle layer or mesoderm is a secondary formation, and is phylogenetically younger than the other two germinal layers; both as regards the origin of its cells and histologically, it is of a compound nature, and thus forms a marked contrast to the two germinal layers proper. One of its first and most important functions is the formation of blood-cells; later it gives rise to the heart, vessels, and to nearly all the supporting and connecting substances (connective tissue, adipose tissue, cartilage, bone), serous membranes (peritoneum,

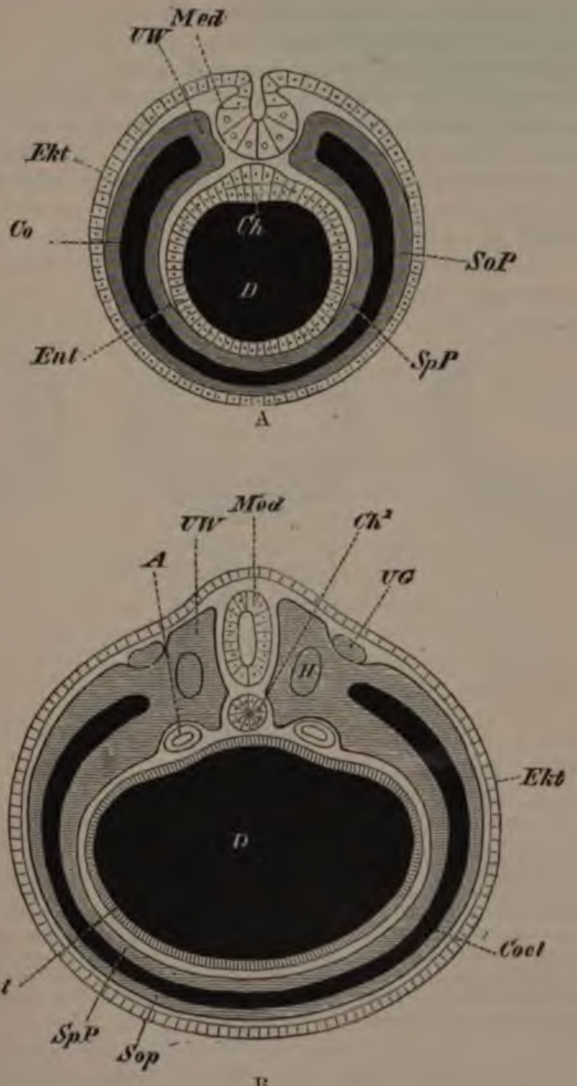


Fig. 6, A and B.—Diagrammatic Transverse Sections through a Developing Vertebrate Embryo.

A, aorta; *Ch*¹, (Fig. B), the notochord now constructed off from the endoderm; *Co*, *Cœl*, cœlome; *D*, alimentary canal; *Ekt*, ectoderm; *Ent*, endoderm, showing in Fig. A the thickening (*Ch*) which will form the notochord; *H*, remains of the upper part of the cœlome in the interior of the mesodermic somites; *Med*, central nervous system (medullary cord):—in Fig. A it is shown still connected with the ectoderm, from which it has become constricted off in Fig. B; *SoP*, somatic, and *SpP*, splanchnic mesoderm; *UG*, primary urinary duct (pronephric duct); *UW*, mesodermic somite.

pleura. pericardium and muscles, as well as to almost the entire excretory and reproductive apparatus.

A space in the mesodermic tissue divides it into a *parietal* or *somatic layer*, lying along the inner side of the ectoderm, and into a *visceral* or *splanchnic layer*, which becomes attached to the outer side of the endoderm (Fig. 6, A and B). The former, together with the ectoderm to which it is united, constitutes the *somatopleure*, and the latter, together with the endoderm, the *splanchnopleure*. The cavity separating these is the body-cavity or *cœlome*, and is lined by an epithelium.

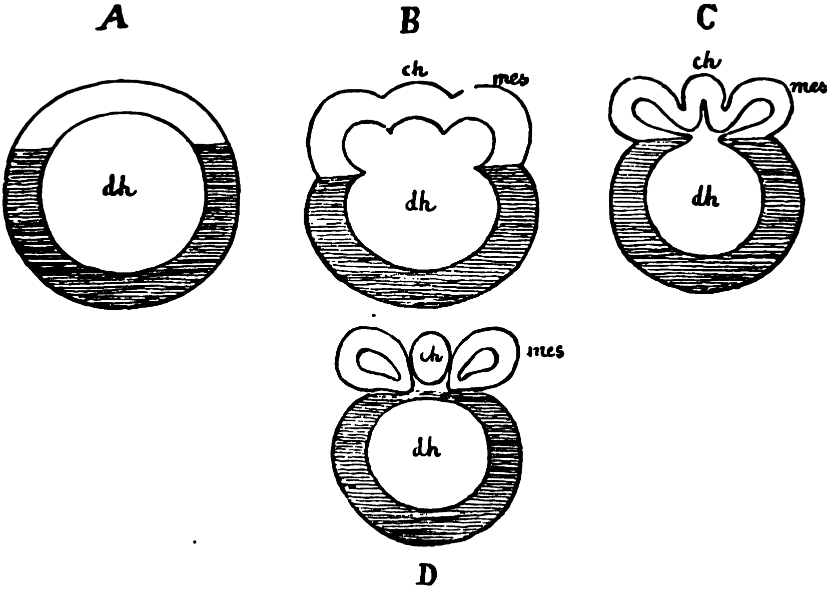


Fig. 7.—Diagrammatic Sections of the Primitive Endoderm and its Derivatives of Amphioxus (A—C, after Götte).

From the dorsal part of the endoderm (unshaded) arise the notochord (*ch*) and the mesodermic somites (*mes*); from the ventral part (shaded), the epithelial lining of the gut. The entire endoderm in stages *B* and *C* thus shows four hollow projections: a median (chordal) and paired lateral (mesodermal) outgrowths communicating at first with the larger ventral intestinal cavity (*dh*), but later becoming constricted off from the latter (*D*). The notochordal outgrowth becomes solid, while the cavities in the mesodermal segments represent the rudiments of the cœlome.

The cœlome may arise as a segmentally arranged series of pouches (*enterocœles*) from the archenteron, in which case its lining epithelium is at first continuous with the endoderm, as is most plainly seen in Amphioxus (Fig. 7); or it may be formed secondarily by a splitting (delamination) of the mesodermic tissue (*schizocœle*). The former of these must be considered as the more primitive.

The dorsal part of the mesoderm which lies on either side of the middle line in all cases early becomes metamerically segmented to form a longitudinal series of *mesodermic somites* or *protovertebræ*, which lose their cavities (cf. Fig. 6, A and B), and are concerned in the formation of the vertebral column, body-muscles, and part of the urinogenital apparatus. This primary segmentation must be distinguished from the segmentation which appears later, on the formation of the vertebral column, ribs, spinal nerves, &c. The ventral parts of the mesoderm are known as the *lateral plates;* in Amphioxus alone do they exhibit segmentation.

As a general rule, a thickened disc-shaped region can be recognised at a certain stage of development on the dorsal pole of the oosperm: this is the so-called *embryonic area*, on which the first indications of the body are seen (Fig. 4). This region gradually sinks into the underlying yolk, from which it becomes constricted off all round by the formation of furrows, and consequently the connection of the body-rudiment with the ventral *yolk-sac* (by the *vitello-intestinal duct*) is gradually reduced in size, and when the yolk is eventually entirely absorbed disappears altogether (Fig. 8, †). In the higher Vertebrates (Reptiles, Birds, and Mammals) folds of the somatopleure arise externally to these furrows, and are known respectively as the *head-*, *tail-*, and *lateral folds*; these gradually grow upwards and eventually unite with one another dorsally so as to form a membranous dome-like sac, the **amnion** (Fig. 8) which encloses the embryo and contains a fluid (*liquor amnii*).

Owing to the presence of this structure, the above-named Vertebrates are usually distinguished as **Amniota** from the **Anamnia** (Fishes and Amphibians), in which no amnion is developed (p. 14).

A network of blood-vessels becomes developed over the yolk-sac, which may therefore serve as an organ of respiration as well as of nutrition. But in the higher Mammals (*Eutheria*) this function is only a very subsidiary one, as at a very early stage a vascular sac-like outgrowth, the **allantois** (Fig. 8), arises from the hinder part of the intestine (*i.e.* from the splanchnopleure). This serves not only for respiration, but also for the reception of excretory matters derived from the primitive kidney. It is also present in Amphibians, but in them remains small, and does not extend beyond the body-cavity of the embryo; while in the Amniota it gradually increases in size and grows round the embryo as a stalked vesicle, which in Reptiles, Birds, and Monotremes comes to lie close beneath the egg-shell and acts as an efficient respiratory organ during the rest of the embryonic period. Towards the close of this period the allantois gradually undergoes more or less complete reduction.

In the higher Mammalia, an important vascular connection takes place between the mother and fœtus by means of the

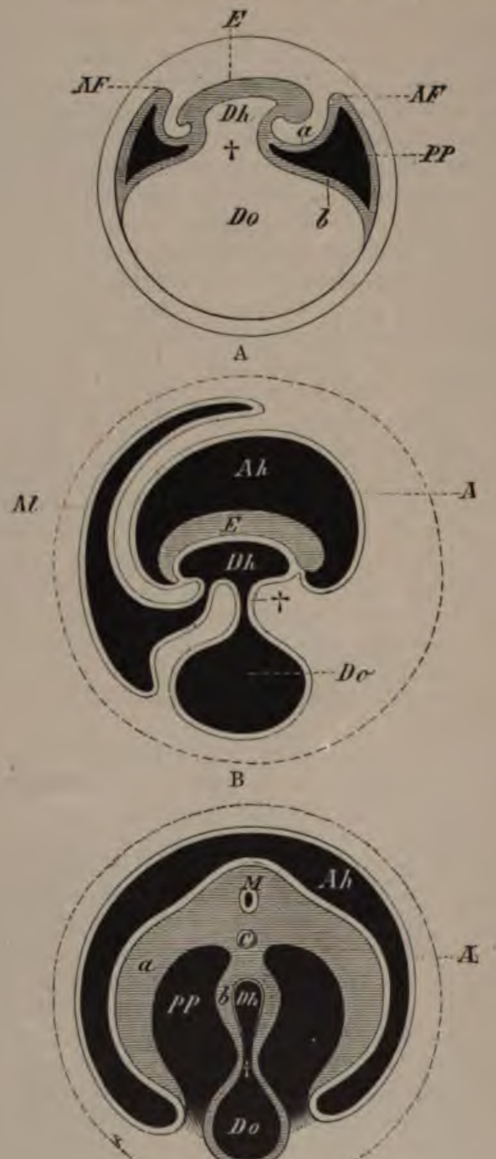


Fig. 8, A, B, and C.—Diagrams illustrating the Formation of the Amnion, Allantois, and Yolk-Sac. A and B, in Longitudinal Section; C, in Transverse Section.

A, amnion; *AF*, amniotic fold; *Ah*, amniotic cavity; *Al*, allantois; *C*, notochord; *Dh*, alimentary cavity; *Do*, yolk-sac; *E*, body of embryo; *M*, medullary cord; *pp*, cœlome; *a*, somatopleure; *b*, splanchnopleure; †, vitello-intestinal duct.

allantois. The latter becomes attached to a definite region of the uterine wall, and from it vascular processes or *villi* arise, so that the fœtal and maternal blood-vessels come into very close relations with one another. Thus an **allantoic placenta** is formed, which serves both for the respiration and nutrition of the fœtus (Fig. 9).

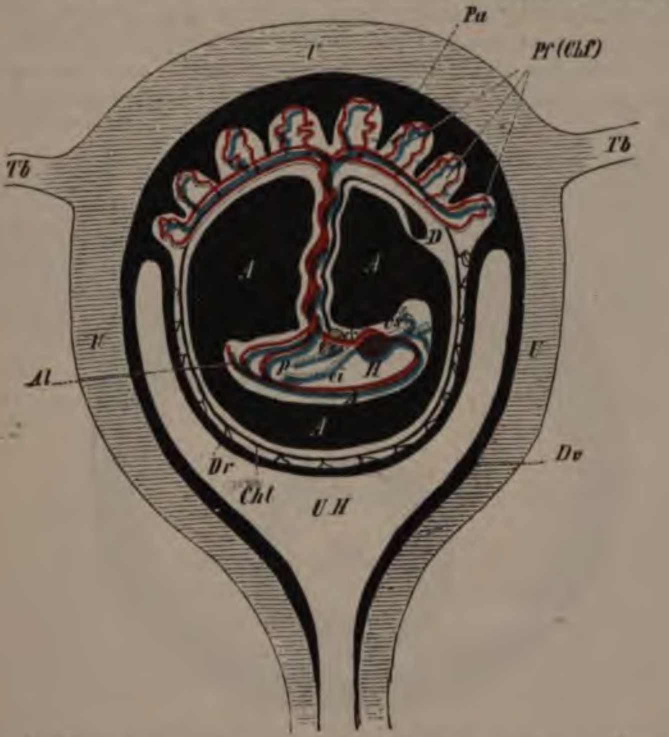


FIG. 9.—DIAGRAMMATIC SECTION THROUGH THE HUMAN GRAVID UTERUS.

A, aorta; *A*, *A*, *A*, the cavity of the amnion filled with fluid: in the interior of the amnion is seen the embryo suspended by the twisted umbilical cord; *Al*, allantoic (umbilical) arteries; *Chl*, chorion læve; *D*, the remains of the yolk-sack (umbilical vesicle); *Dr*, decidua reflexa; *Dv*, decidua vera, which at *Pu* passes into the uterine portion of the placenta; *H*, heart; *Pf*, fœtal portion of the placenta (chorion frondosum, *Chf*); *Tb*, Fallopian tube; *U*, uterine wall; *UH*, uterine cavity; *ci*, postcaval, *cs*, precaval, and *p*, portal vein; †, the liver, perforated by the umbilical vein.

The following important points must now be noted as regards the structure of the Vertebrate body. After the above-mentioned main organs have appeared, a smaller dorsal **neural tube** and a larger ventral **visceral tube** are seen to extend longitudinally through the body, and between the two is a rod-like supporting structure, the **notochord** (p. 6), which forms the primary skeletal axis; it is usually replaced by a **vertebral column** consisting of *vertebræ*, at a later stage of development (Fig. 10). All these structures are median in position, and the body is thus *bilaterally symmetrical.* The neural tube, or *cerebro-spinal cavity*, enclosed by the *skull* and *arches of the vertebræ*, contains the *central nervous system* (*brain* and *spinal cord*); the visceral tube (*cœlome*) encloses the *viscera* (alimentary canal, heart, urinogenital organs, &c.), and its muscular walls may be strengthened by a series of *ribs*, articulating dorsally with the vertebral column.

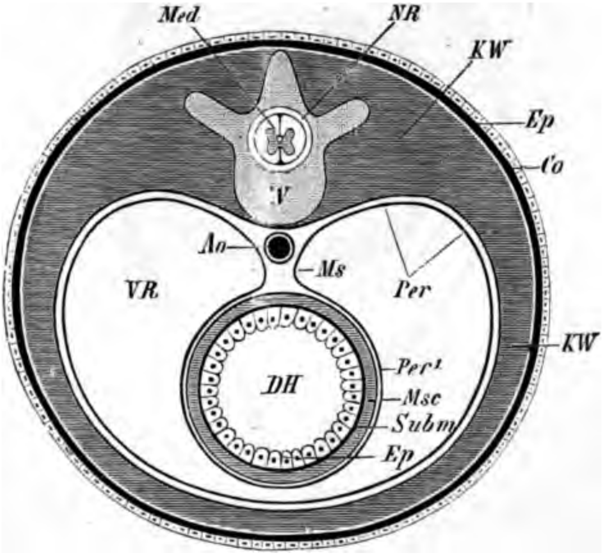


FIG. 10.—DIAGRAMMATIC TRANSVERSE SECTION THROUGH THE BODY OF AN ADULT VERTEBRATE.

Ao, aorta; *Co*, derm; *DH*, lumen of intestine; *Ep*, endodermic epithelium of intestine; *KW*, body-wall; *Med*, spinal cord; *Ms*, mesentery; *Msc*, muscular coat of intestine; *NR*, neural tube; *Per*, parietal layer of the peritoneum; *Per*[1], visceral layer of the peritoneum; *Subm*, connective-tissue coat of intestine; *VR*, visceral tube; *W*, vertebra.

Certain of the ribs may reach the mid-ventral line and come into connection with a *breast-bone* or *sternum*, and thus form complete rings or hoops around the visceral tube.

The anterior end of the central nervous system (brain) and of the alimentary tract enter into close relations with the outer world, the former being connected with the higher sense-organs, while from the latter are developed the mechanisms for taking in nutriment and for respiration.

The anterior portion of the body, or *head*, passes behind into the *trunk*, either with or without the intermediation of a *neck*. The *cœlome* is practically restricted to the trunk, in the hinder part of which the intestinal (anal) and urinogenital apertures are situated, and posterior to which again is the *tail*. Head, trunk, and tail constitute the **body-axis,** as distinguished from the *fins* or *limbs* **(appendages),** which arise from the trunk and of which there are typically two pairs. In addition to the paired appendages, median fins are present in aquatic forms.

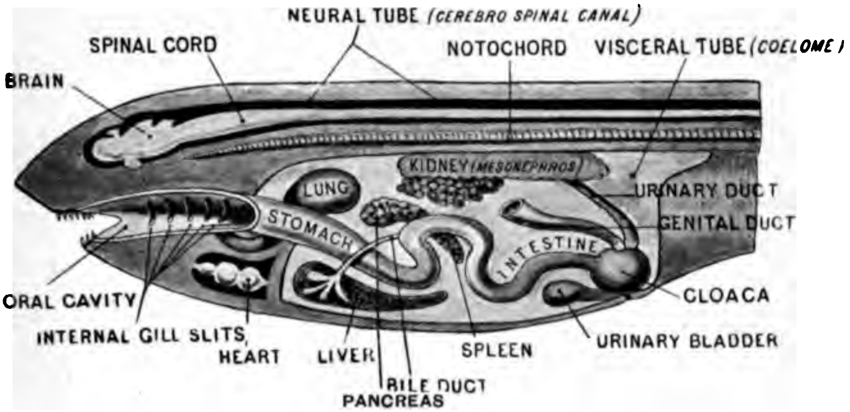


FIG. 11.—DIAGRAMMATIC LONGITUDINAL SECTION OF A VERTEBRATE (♀).

SYSTEMATIC ZOOLOGY is concerned with the classification of animals, on the basis of their relationship to one another, into certain divisions and subdivisions, the chief of which are designated as *Phyla*, *Classes*, *Orders*, *Families*, *Genera*, and *Species*. In this connection, structural resemblance (*homology*) is taken into account, and not mere functional resemblance (*analogy*).

A general classification of the principal Vertebrate groups, sufficient for the purposes of this book, and also a table showing the order of their appearance in past time, are given on the following pages.

Division A. ACRANIA (CEPHALOCHORDATA).
Lancelet (Amphioxus).

,, B. CRANIATA.

GNATHOSTOMATA.

ICHTHYOPSIDA.

a. ANAMNIA.
Class I. CYCLOSTOMATA (Suctorial Fishes).
Order 1. *Myxinoidei* (Hag Fishes—Myxine, Bdellostoma).
,, 2. *Petromyzontes* (Lampreys).
Class II. PISCES (True Fishes).
Sub-class 1. ELASMOBRANCHII.
Order 1. *Plagiostomi* (Sharks—Selachii, and Rays—Batoidei).
,, 2. *Holocephali* (Chimæra, Callorhynchus).
Sub-class 2. TELEOSTOMI.
Order 1. *Crossopterygii* (Polypterus, Calamichthys).
,, 2. *Chrondrostei* (Acipenser, Polyodon).
,, 3. *Holostei* (Lepidosteus, Amia).
Ganoidei.
,, 4. *Teleostei.*
Sub-order *a.* *Physostomi* (Carp, Pike, Salmon, Herring, Eel, Siluroids).
,, *b.* *Anacanthini* (Cod, Flat-fishes).
,, *c.* *Acanthopteri* (Perch, Stickleback, Gurnard, Blenny).
,, *d.* *Pharyngognathi* (Wrasse).
,, *e.* *Plectognathi* (Trunk- and File-fishes).
,, *f.* *Lophobranchii* (Pipe-fish, Sea-horse).
Physoclisti.
Sub-class 3. DIPNOI.
Order 1. *Monopneumona* (Ceratodus).
,, 2. *Dipneumona* (Protopterus, Lepidosiren).
Class III. AMPHIBIA.
Order 1. *Urodela.*
a. *Perennibranchiata* (Proteus, Siren, Necturus).
b. *Caducibranchiata* { *Derotremata* (Amphiuma, Menopoma).
Myctodera (Salamandra, Triton, Amblystoma).
,, 2. *Anura* (Frogs and Toads).
,, 3. *Gymnophiona* (Limbless Cæcilians).

SAUROPSIDA.

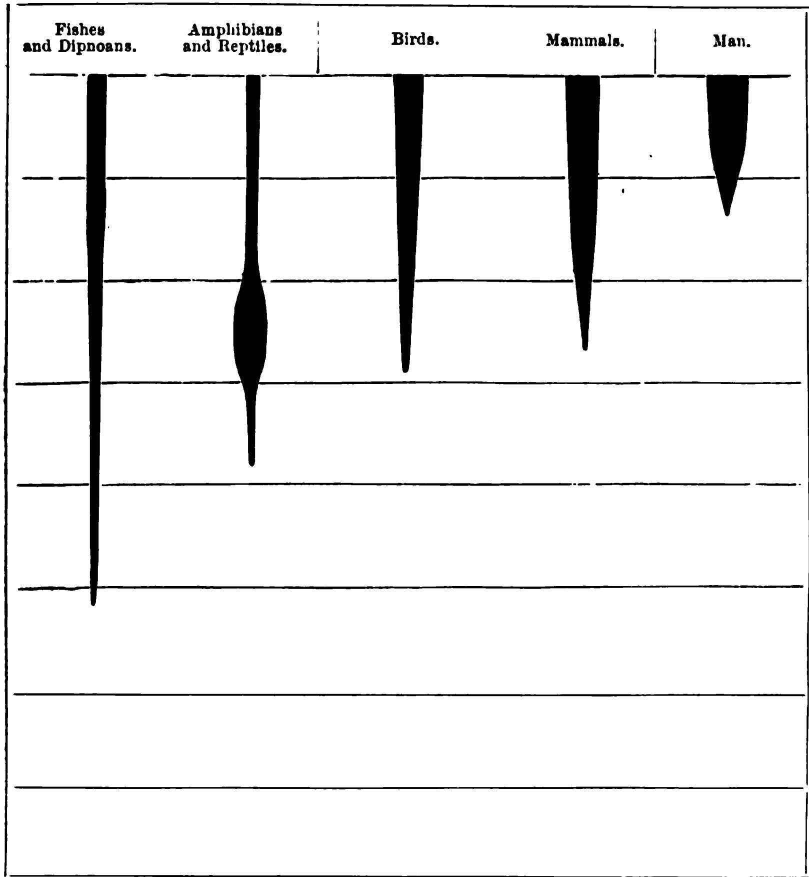
β. AMNIOTA.
Class IV. REPTILIA.
Order 1. *Rhynchocephali* (Hatteria).
,, 2. *Lacertilia* (Lizards).
,, 3. *Ophidia* (Snakes).
,, 4. *Chelonia* (Turtles and Tortoises).
,, 5. *Crocodilia* (Crocodiles and Alligators).
Class V. AVES.
a. *Ratitæ* (Cursorial Birds—Ostrich, Rhea, Emu, &c.).
b. *Carinatæ* (Birds of Flight).

Class VI. MAMMALIA.
Sub-class 1. PROTOTHERIA or ORNITHODELPHIA (the Oviparous Monotremes — Ornithorhynchus, Echidna).
,, 2. METATHERIA or DIDELPHIA (Marsupials—Kangaroo, Phalanger, Opossum.).
,, 3. EUTHERIA or MONODELPHIA.

GNATHOSTOMATA.

Order 1. *Edentata* (Sloth, Anteater).
,, 2. *Sirenia* (Dugong, Manatee).
,, 3. *Cetacea* (Porpoise, Whale).
,, 4. *Ungulata* (Rhinoceros, Horse, Ruminants.)
,, 5. *Hyracoidea* (Hyrax).
,, 6. *Proboscidea* (Elephant).
,, 7. *Rodentia* (Rabbit, Mouse, Beaver, Cavies).
,, 8. *Cheiroptera* (Bats).
,, 9. *Insectivora* (Shrew, Mole, Hedgehog).
,, 10. *Carnivora* (Bear, Dog, Cat, Seal).
,, 11. *Prosimii* (Lemurs).
,, 12. *Primates* (Monkeys and Man).

TABLE SHOWING THE GRADUAL DEVELOPMENT OF THE VERTEBRATA IN TIME. MODIFIED FROM H. CREDNER.



Period.	Formation	
Of the prevalence of warm-blooded animals, particularly Man.	Recent.	Kainozoic
Of the prevalence of Mammals: the first Man.	Quaternary. Tertiary.	
Of the maximum development of Reptiles: the first Birds and Mammals.	Cretaceous. Jurassic. Triassic.	Mesozoic
Of the first Amphibians and Reptiles.	Permian. Carboniferous.	Palæozoic
Of tolerably numerous Fishes (armoured Ganoids).	Devonian.	
Of the first Fishes.	Upper Silurian	
	Lower Silurian Cambrian.	
	Archæan.	

SPECIAL PART.

A. INTEGUMENT.

THE **skin** consists of a superficial ectodermal layer, and a deeper mesodermal layer. The former is called the **epiderm** (scarf-skin) and the latter the **derm** (*corium, cutis*).

In the *epiderm*, which consists of cells only, two parts may in general be distinguished:—an external layer, composed of flattened and hardened cells (*stratum corneum, horny layer*), and a deeper, of more columnar, formative cells (*stratum Malpighii* s. *germativum, mucous layer*). The latter serves for the regeneration of the horny layer, the superficial part of which is continually scaling off, as well as for the formation of such *horny structures* as hairs, bristles, nails, claws, and hoofs, and of the *integumentary glands*. The *peripheral sensory end-organs* also arise by a differentiation of this layer of cells.

The *derm*, which is usually thicker and tougher than the epiderm, is made up principally of connective tissue and smooth muscular fibres: it is usually not sharply marked off from the subcutaneous connective tissue, which commonly encloses more or less fat. Externally, the derm may give rise to numerous papillæ projecting into the epiderm, especially in higher forms. Apart from the horny and glandular structures extending into it from the epiderm, the derm encloses *vessels, nerves*, and often *bony structures* also.

Pigment cells (*chromatophores*) and free pigment occur in both layers of the skin: they correspond to modified connective tissue cells, and in them a temporary shifting of the contained pigment may occur, this process being under the control of the nervous system.

In **Amphioxus,** the epiderm differs from that of all the Craniata in the fact that it consists of a single layer of cells: its surface is covered with cilia in the larval (gastrula) stage, and this must undoubtedly be considered as an inheritance from Invertebrate ancestors.

Fishes.

The character of the epiderm varies greatly in the different groups (Fig. 12). The striated cuticular border (present *e.g.* in Cyclostomes, Teleosts, and Dipnoans) possibly indicates the former possession of cilia.[1] Cornification of the superficial layer occurs, especially in Teleosts, over those parts of the scales (Fig. 13) which are not overlapped by their fellows. Numerous lymph-cells (leucocytes) are found in the epiderm which have wandered out of the derm, and some of them contain pigment. The derm consists mainly of horizontal and vertical layers of connective tissue, and encloses the other structures already referred to (Figs. 12 and 13).

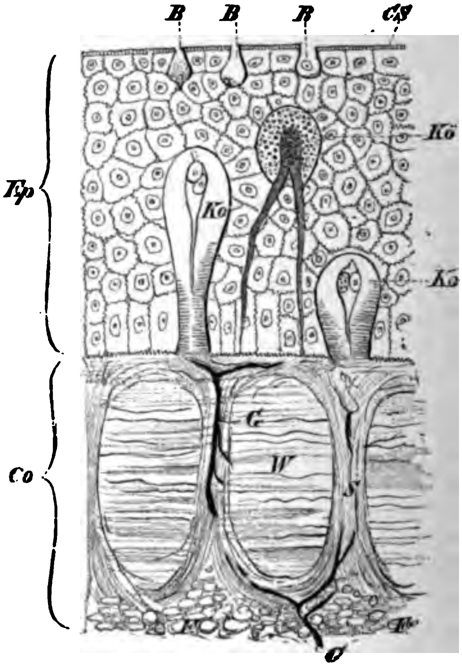


FIG. 12.—DIAGRAMMATIC TRANSVERSE SECTION ILLUSTRATING THE STRUCTURE OF THE SKIN IN FISHES.

B, *B*, goblet-cells opening on the surface; *Co*, derm; *CS*, cuticular margin; *Ep*, epiderm; *F*, subcutaneous fat; *G*, vessels which pass upwards in the vertical connective tissue bundles (*S*) of the derm; *Ko*, goblet-cells; *Kö*, granular cells; *W*, horizontal connective-tissue bundles.

Various kinds of mucus-secreting cells are formed in the epiderm, and in addition to the relatively larger or smaller *goblet*

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[1] Cilia are occasionally present in very early stages in Teleosts.

cells commonly present may be mentioned the *granular cells* in the Lamprey (the nature of which is not understood), and in Myxinoids the numerous *slime-sacs*, formed as invaginations of the epiderm and containing peculiar *thread-cells*.

Special aggregations of gland-cells occur in relation with the copulatory organs or claspers of male Elasmobranchs (*glandulæ pterygopodii*), and on the operculum and dorsal fin-rays of certain Acanthopteri (*e.g.* Trachinus, Thalassophryne, Synanceia), in which latter they constitute a *poison-apparatus* serving for offence or defence, and consist of modified epidermic cells enclosed in grooves of the spines of the operculum and dorsal fins. Most of these poison-fishes are inhabitants of the temperate and warmer seas: in fresh-water forms (*e.g.* Perca, Cottus), the apparatus has apparently undergone partial or total degeneration. Poison-organs are also said to occur in a number of other Teleosts (*e.g.* in connection with the dorsal and pectoral spines of many Siluridæ) and in certain Elasmobranchs; a closer examination will probably prove their existence in many other Fishes.

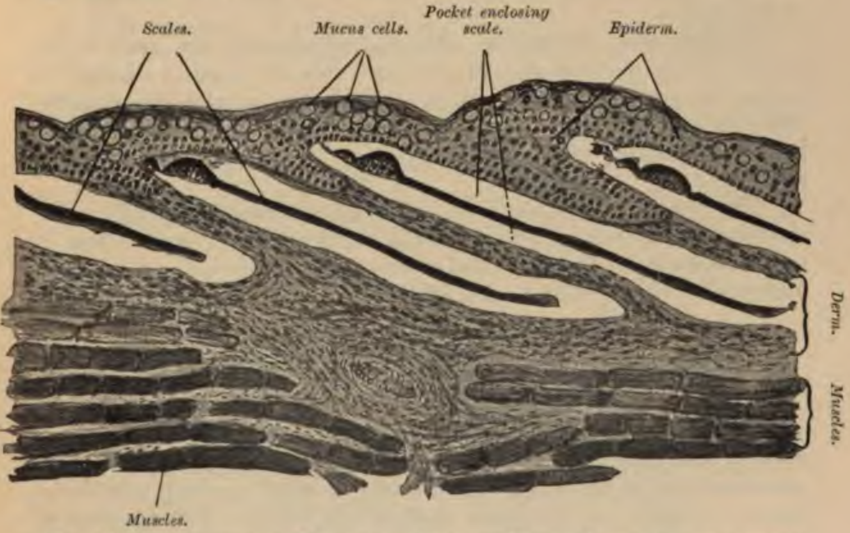

FIG. 13.—LONGITUDINAL SECTION OF SKIN OF YOUNG TROUT (15 CM. LONG), FROM THE TAIL.

Phosphorescent organs, formerly known from their appearance as "accessory eyes," occur on various parts of the head, body, and tail of several families of deep-sea Teleosts (*e.g.* Stomiatidæ, Halosauridæ, Anomalopidæ), and in certain species of Elasmobranchs belonging to the family Spinacidæ. Their arrangement, distribution, and structure is very varied in different forms. The luminous part consists of gland-cells, supplied by the trigeminal, facial, and spinal nerves; and a number of accessory parts may be present, *e.g.* a pigment-layer, a reflecting apparatus, a vitreous body, and structures resembling a lens and an iris. These organs probably serve to attract prey or to help their possessors in seeking food in the darkness of the deep sea.[1]

In addition to very numerous goblet-cells, the epiderm of the South African Dipnoan, Protopterus, gives rise to cup-shaped *multicellular glands*, resembling those of the Amphibia. During the dry season, this animal (like its South American ally, Lepidosiren[2]), buries itself in the river-bottom: its integumentary glands then produce a varnish-like secretion and an enclosing cocoon or capsule, by means of which it is protected during the torpid period.

Pigment-cells, which, as already mentioned, are under the control of the nervous system, and are able to cause a change of colour, are present sometimes in both layers of the integument, sometimes in one only. Colour may also be produced by reflecting bodies consisting of excretory products (guanin) and known as *iridocytes.*

The presence of *scales* (see under Exoskeleton) may affect the epiderm when they project from the surface, and in some cases it may disappear so that the scales become superficial (*e.g.* in Elasmobranchs, Ganoids, and some Teleosts).

Amphibians.

The epiderm of. Amphibians differs markedly from that of Fishes, inasmuch as nearly all the special forms of cells so characteristic of the latter are wanting. Both epiderm and derm, moreover, differ in the larva and in the adult. The epiderm at first consists of a single layer of cells, and then of two layers, the superficial one being provided with a ciliated or a striated cuticular border,[3] and remaining throughout the larval period as a covering layer (Fig. 14). The deeper layer, on the other hand, undergoes various modifications: it becomes stratified, and replaces the superficial cells as they are lost. Slime-secreting goblet-cells, such as are characteristic of the epiderm of fishes, are typically wanting,[4] and leucocytes are not abundant. Unicellular glands, known in Urodeles as *Leydig's cells*, are, however, abundant in the larva;

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[1] For the electric organs of Malopterurus, which are said to be epidermic in origin, cf. under *Electric Organs.*

[2] In the breeding season the posterior extremities of the male Lepidosiren are provided with numerous long vascular papillæ.

[3] Cilia occur abundantly in Salamander larvæ over parts of the head and body, and their distribution is related to that of the integumentary sense-organs; they are also found in very young Anuran larvæ.

[4] In older Urodele larvæ, after the epiderm has become thickened, numerous goblet-like cells can be recognised and probably represent the Leydig's cells described above.

and cells with thread-like and vacuolated contents have also been described in Anuran larvæ. Later on, immediately before metamorphosis, numerous *multicellular glands* of alveolar structure

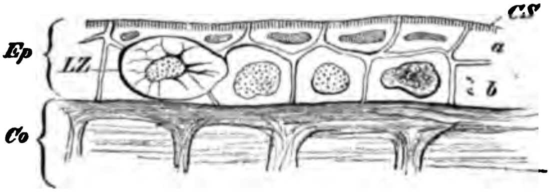

FIG. 14.—SKIN OF LARVA OF SALAMANDER (*Salamandra maculosa*).

a, stratum corneum; *b*, stratum Malpighii; *Co*, derm; *CS*, striated border; *Ep*, epiderm; *LZ*, Leydig's cells (unicellular mucus glands).

(cf. p. 20) appear in adaptation for terrestrial life. These have nothing to do with the unicellular larval glands: their great abundance is very characteristic of the Amphibian skin (Figs. 15 and 16). As regards their distribution, they may be scattered singly throughout the skin, or arranged in groups—in Anurans chiefly

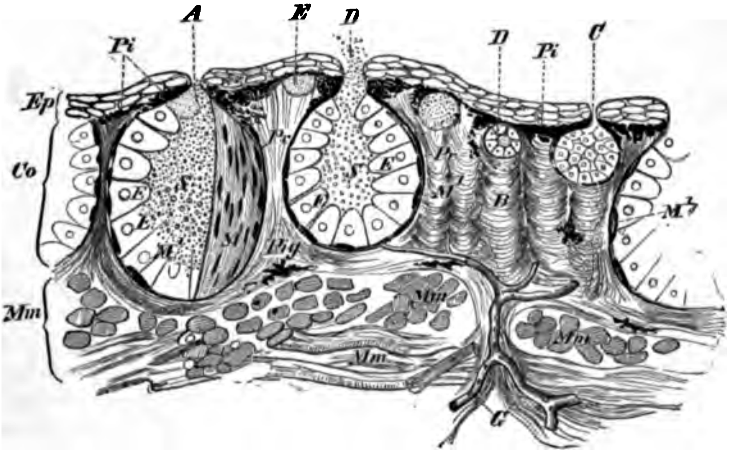

FIG. 15.—SEMIDIAGRAMMATIC SECTION THROUGH THE SKIN OF ADULT SALAMANDER (*S. maculosa*).

Co, derm, in the connective tissue stroma of which (*B*) the various sized integumentary glands (*A*, *C*, *D*, *D*) lie embedded; *E*, epithelium of glands; *Ep*, epiderm; *M*¹, the muscular, and *Pr* the connective-tissue layer of the glands; *M*, the same, seen from the surface; *Mm*, subcutaneous layer of muscles, through which vessels (*G*) extend into the derm; *Pi*, *Pig*, pigment cells in the derm; *S*, secretion of glands.

along the back, in Urodeles (and Toads) at the junction of head and trunk ("*parotoids*") or laterally along the body and in the caudal region (*e.g.* Spelerpes, Plethodon). These aggregated glands vary not only in relative size, but also in the structure of their cells and in function. *Mucus-glands*, and much larger *poison-glands* (the secretion of which is granular), can usually be distinguished, the latter serving as a passive means of defence; but intermediate forms may be recognised. Smooth muscle-cells are very numerous in the derm, certain of them surrounding these glands, and forming constrictors and dilators.

In the Anura, the blood-vessels are not always confined to the derm, but in connection with the respiratory function of the skin extend far into the epiderm before metamorphosis, during which process the capillary loops in the epiderm increase markedly, decreasing again subsequently. This may be explained by the fact that during metamorphosis the gills are no longer functional and pulmonary respiration alone is apparently insufficient; an additional vicarious arrangement is therefore temporarily necessary.

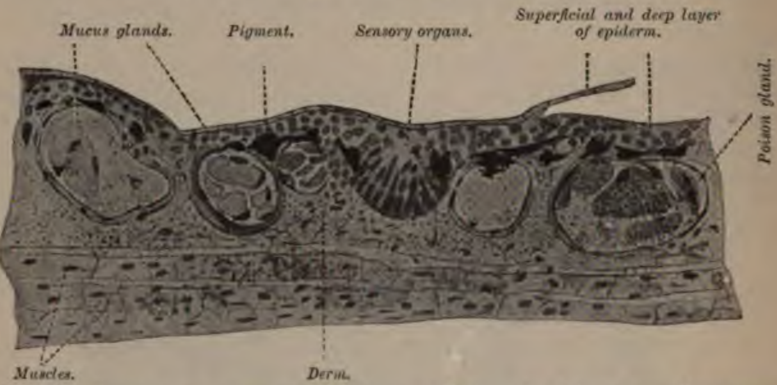

FIG. 16.—SECTION THROUGH THE SKIN OF A *Triton alpestris* IN THE BREEDING SEASON.

The coloration of the skin, which may undergo change, is due to *chromatophores* of different tints in the derm. The derm is similar to that of Fishes, and is, moreover, characterised by an abundance of blood-vessels and nerves, as well as of smooth muscle-fibres. *Calcifications* and even *ossifications* (*e.g.* in Ceratophrys dorsata) may occur in the derm, and in the Gymnophiona definite dermal *scales* are present.

A stratified stratum corneum becomes developed even in perennibranchiate types, and may become more pronounced in adaptation to a terrestrial existence in caducibranchiate forms at metamorphosis. The cornification is especially marked along the back, and may result in the formation of warts and papillæ; occasionally claw-like structures are developed on the digits (Xenopus, Onychodactylus). The horny layer of the epiderm is shed periodically, either in pieces or entire.

Reptiles.

In adaptation from the first to a terrestrial in place of an aquatic existence, the skin of Reptiles is dry and more or less pneumatic. Integumentary glands are practically wanting. The "femoral pores" of Lizards, which were formerly looked upon as glands, are now known to be merely subcutaneous, branched, tube-like cavities lined by cornified cells which project from the pores in the form of solid cones, and possibly serve as clasping organs during copulation: it is doubtful whether these structures originated from glands in the first instance. In the Crocodilia a row of about twenty small, gland-like sacs are present under the skin along the back from the neck to the base of the tail, at the boundary between the first and the second rows of scutes. Nothing is known as to the function of these, or of the evaginable and odoriferous "musk-gland" on the lower jaw of Crocodiles and the invaginations of the integument on the margins of the carapace in Chelonians.

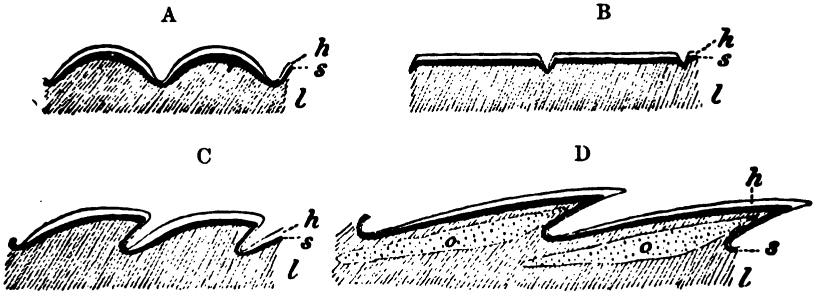

FIG. 17.—DIAGRAMMATIC SECTIONS THROUGH VARIOUS KINDS OF EPIDERMIC SCALES OF REPTILES. (From Boas's *Zoology*.)

A, rounded scales; *B*, shields; *C*, imbricating scales; *D*, the same, with bony scutes in the underlying derm; *h*, horny layer, and *s*, Malpighian layer of the epiderm; *l*, derm; *o*, bony scutes.

A further characteristic difference between the skin of Reptiles and that of most Amphibians is seen in the presence of *scales* (Fig. 17). Horny epidermic scales and dermal bony structures, both of which may be present in the same animal, must be distinguished from one another (D). In all cases, the first traces of the scales are due to the formation of dermal papillæ, which may or may not become calcified or ossified. In the former case, the resulting bony scale or scute still remains covered by the more or less horny epiderm (*e.g.* Anguis, Scincidæ). As a general rule, the epidermal cornification is much more marked than the ossification.

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The dermal papilla is thus always the primary part of the scale which causes the elevation of the epiderm (Fig. 18). At the same time, a marked proliferation of the epiderm occurs, at first uniformly and later in different degrees on the upper and lower surfaces of scales when they overlap one another (Fig. 19).

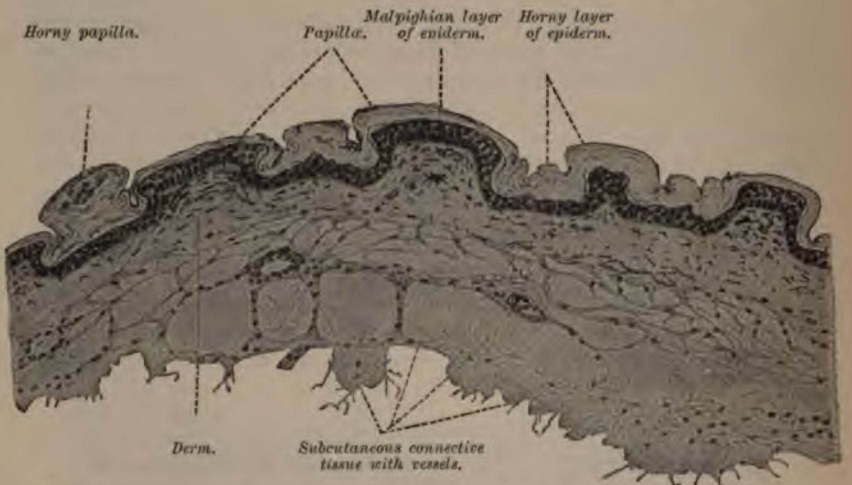
Horny papilla.
Papillæ.
Malpighian layer of epiderm.
Horny layer of epiderm.
Derm.
Subcutaneous connective tissue with vessels.

Fig. 18.—Section of Skin of a Young Tortoise (*Testudo græca*), from the Neck.

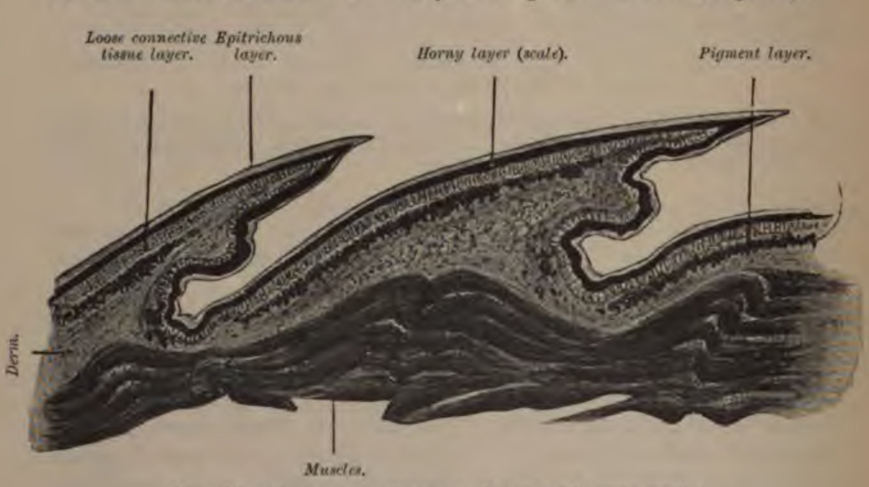

Fig. 19.—Section of Skin of Lizard (*Lacerta agilis*).

As in Amphibians, a periodic casting of the superficial part of the many-layered horny epiderm occurs, either in shreds, or entire (*e.g.* Snakes, Anguis). Most Lizards simply creep out of their cast skin, as out of a sack; while in Snakes it becomes turned inside out while being shed.

The horny substance may undergo a variety of modifications, and may give rise to such structures as ridges, prickles, warts, claws, shields (*e.g.* the "tortoiseshell" of Chelonians[1]), and rattles (Rattlesnakes); or it may develop bunches of cuticular hair-like bodies, such as those found on the toe-discs of Geckos.

In the derm, a superficial and a deeper layer may be distinguished. The latter is composed mainly of strong bundles of connective tissue fibres which as a rule cross one another at right angles, as in Fishes and Amphibians. The superficial or subepidermic layer is looser in structure, and in addition to connective tissue fibres, encloses smooth muscles and chromatophores (Fig. 19), the degree of development of the latter differing greatly: several rows of them may be present, *e.g.* in the Chameleon. The power of changing colour, so characteristic of the last-named, is, however, possessed to a greater or less extent by many other Reptiles.

Birds.

The skin of Birds is characterised by giving rise to *feathers*, as well as by the relatively thin epiderm and derm, the connective tissue fibres of the latter being irregularly felted. A *uropygial gland*, peculiar to Birds, and situated at the base of the rudimentary tail (uropygium) is present in nearly all, being wanting only in a few groups (*e.g.* Ratitæ): its secretion serves to oil the feathers, and it is especially well developed in Water-Birds. A gland is also present in the neighbourhood of the auditory passage in certain Gallinaceæ, but otherwise integumentary glands are wanting in Birds. Characteristic of the derm is its richness in sensory organs (*tactile corpuscles*) and muscle-fibres, most of which latter are inserted into the feather-sacs and serve to erect the feathers (*arrectores plumarum*). Epidermic scales are present on the feet.

The feather is foreshadowed in the reptilian epidermic scale, of which it is merely a further modification. That scales and feathers are homologous structures is, at any rate to a certain extent, indicated by their mode of development, which is briefly as follows.

In the region where a feather is to be formed, the dermal tissue becomes slightly raised up towards the thickened epiderm (Fig. 20, A), and thus gives rise to a vascular papilla. As this papilla grows out to form an elongated cone, the *feather-germ* (B), its vascular base gradually sinks deeper and deeper into the derm, and thus becomes surrounded by a sort of pocket—the *feather-follicle.* The horny, as well as the Malpighian layer of the epiderm extends into the base of the follicle, and thence on to the feather-germ, the interior of which is throughout filled by cells of the derm which give rise to the *pulp.*

---

[1] The individual epidermic shields of Chelonians are independent of the underlying bony plates (Fig. 33), and do not correspond with them in arrangement.

As the feather-germ keeps on growing, the cells of the Malpighian layer begin to proliferate rapidly, giving rise to a series of radial folds arranged along a central axis and extending inward towards the pulp (Fig. 21, A). These folds, between which the nutritive pulp extends, then become cornified and separated from above downwards from the surrounding cells (B); and, on a gradual drying of the central pulp-substance, give rise to a tuft of horny rays (C), which are, however, at first bound together by the enclosing stratum corneum, which forms a sheath around them. Most Birds are hatched when the feathers are in this stage of development, and they thus appear as if covered with brush-like hairs.

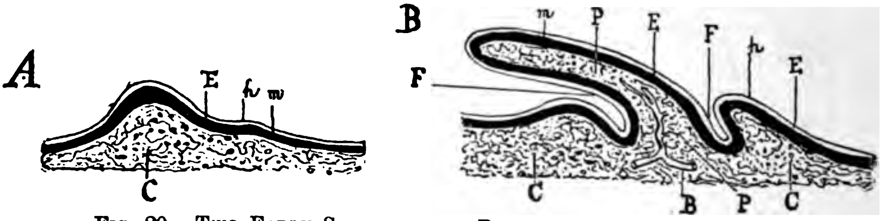

Fig. 20.—Two Early Stages in the Development of the Feather (Semidiagrammatic).

B, blood-vessel; *C*, derm; *E*, proliferating epiderm; *F*, rudiment of follicle; *h*, horny, and *m*, Malpighian layer of epiderm; *P*, pulp of the papilla.

By the shedding of the investing horny sheath, the rays or *barbs*—on which smaller secondary rays or *barbules* become developed—become free, and thus an embryonic *down-feather* (*pluma*) is formed. The whole feather-germ, however, does not become divided up in this manner: its lower portion, embedded in the skin, forms the *quill* (*calamus*), the interior of which contains a peculiar flaky and air-containing horny substance, the dried remains of the pulp.

Thus the earlier stages of development of the feather and reptilian scale are very similar, but during later stages the feather becomes adaptively specialised. The warm-blooded but still flightless ancestors of Birds probably possessed a covering of down-feathers which served as a protection against the cold, and which only later become adapted in connection with flight.

In many Birds the feathers retain throughout life the essential characters of down, with more or less differentiation (*e.g.* Ratitæ, and more especially the Cassowaries); but in most cases the down[1] becomes covered or replaced by the more complicated definitive *contour-feathers*, the proximal barbs of which usually still retain their down-like character. A contour-feather (*penna*) at first closely resembles a down-feather, but in the course of further growth, two adjacent rays become enlarged to form, with the relatively longer or shorter quill, a main axis or stem (*scapus*): the part distal to the quill, to which the barbs are attached in a double row opposite one another is called the shaft (*rachis*). At the base of the quill is a small aperture, into which the vascular papilla extends; and a second very small aperture is present at the junction of quill and shaft on the inner surface.

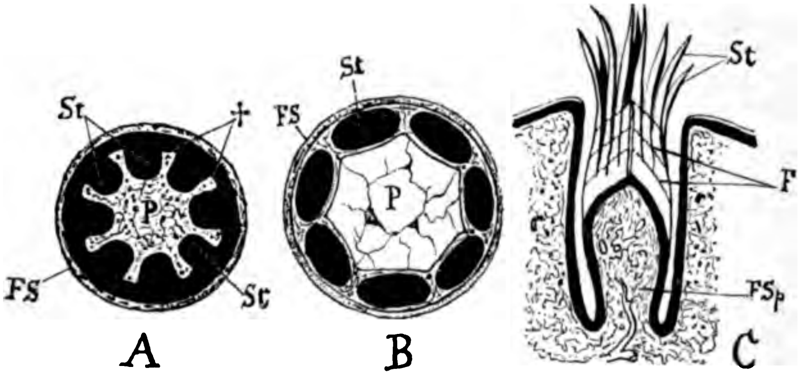

FIG. 21.—THREE STAGES IN THE DEVELOPMENT OF THE EMBRYONIC DOWN DIAGRAMMATIC (after Davies). A, B, IN TRANSVERSE, and C IN LONGITUDINAL SECTION.

F, dried remains of pulp; *F.S*, follicle; *F.Sp*, quill; *P*, pulp, with its extensions towards the feather sheath at † in A, which separate the developing barbs (*St*): these have become free in C.

The barbs together constitute the vane (*vexillum*), and the barbules arise obliquely, in a double row on each barb, so as to have relations to the latter similar to those of the barbs to the shaft. On the barbules a double series of *barbicels* are developed, certain of which may bear minute hooklets which interlock with one another, and so connect the barbs together into a continuous sheet: this is particularly the case in the row of large wing-feathers (*remiges*) on the fore-arm and manus and of tail-feathers (*rectrices*) on the rump or uropygium.

In many Birds each quill of the ordinary feathers of the body bears two vexilla, which may be equal in size (Cassowary); but usually one, the aftershaft (*hyporachis*), is smaller than the main shaft.

---

[1] Various modifications of the down feathers occur (*e.g. filoplumes*, which by some zoologists are supposed to represent the last remains of a primitive feather-covering from which both down-feathers and contour-feathers have become differentiated).

The contour feathers are generally not distributed irregularly over the body, but are arranged in definite feather-tracts (*pterylæ*) separated by down-covered spaces (*apteria*), having a more or less different arrangement in the various groups.[1]

A periodic casting of feathers, or *moulting*, takes place in all Birds, and corresponds to the similar process of the casting of the horny epidermic layer in Amphibians and Reptiles: the papilla persists, and in connection with it the replacing feather is developed.

The feather-covering of Birds must have been acquired in very early geological periods, for Archæopteryx, found in the Jurassic strata of Bavaria, possessed well-formed feathers with a delicate shaft and vane (Fig. 49).

The colours of feathers are due in part to the presence of various pigments (viz., red, yellow, orange, black, and brown), and in part to the phenomenon of interference, which may produce white, grey, blue, and metallic or iridescent tints.

Mammals.

The integument of Mammals is characterised by the presence of *hairs*, and the question as to how far scales, feathers, and hairs are comparable to one another is an interesting one. No intermediate forms are known, but there is no doubt that the feather is much nearer to the scale than is the hair. The study of their development, however, shows that the origin both of hair and feather may be traced in the first instance to similar scale-like structures, in spite of their very different final form. Thus phylogenetically both are closely related to the horny scales of Reptiles.

The development of hairs, as well as their grouping and distribution, indicates certain topographical relations to scales, and also that they first arose in relation with a primitive scaly coat. Secondarily they appeared on or behind the scales, which were gradually reduced as the hairs underwent increasing differentiation. Hairs, which, like feathers, are arranged in groups, are not, however, individually homologous with scales, but arise from parts of a scale-area, while the feather possibly corresponds to an entire scale. There can be little doubt that the earliest Mammals, which arose from primitive Reptiles, possessed an extensive scaly covering in addition to a sparse coat of hairs.

In development, the first essential indication of the hair is seen in the epiderm, which may or may not become raised up at the point in question[1] (Fig. 22). This thickening of the epiderm grows downwards in the form of a papilla (*hair-germ*) and is surrounded by the cells of the derm, so that, as in the case of the feather, it comes to lie within a kind of pocket, the *hair follicle*. The originally uniform mass of cells of the hair-germ is later differentiated into a peripheral and a central portion: the latter (*bulb-cone*, C) gives rise later (D) to the *hair-shaft* with its *medulla* and *pith*, and to the *cortex*, as well as to the *cuticle* of the shaft and the so-called *inner root-sheath*; from the former arises the *outer root-sheath*. The origin of both sheaths, as well as the *sebaceous glands*, can be traced to the Malpighian layer (cf. Fig. 23.) The base of the hair-shaft which fills up the bottom of the follicle is broadened out to form the *hair-bulb*, which extends round the highly vascular hair-papilla like a cap. The hair usually breaks through the skin obliquely, the direction differing in different parts of the body.

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[1] In some Birds bristle-like feathers occur on the head, and the foot-scales or shields may bear feathers of a peculiar form. In insectivorous and nocturnal forms, *tactile* or *sinus-feathers* are present around the eye and ear and at the base of the beak, analogous to the sinus-hairs of Mammals (*q.v.*).

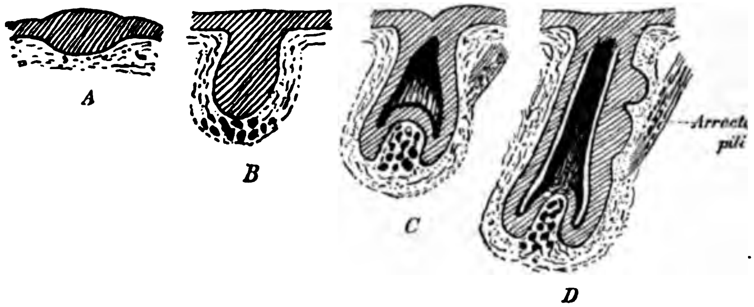

FIG. 22.—DIAGRAM OF FOUR STAGES IN THE DEVELOPMENT OF THE HAIR (founded on Stöhr's figures).

A, hair germ; *B*, hair-cone; *C*, bulb-cone, showing formation of bulb, papilla, and hair-cone, which latter is becoming cornified at the apex. *D*, later stage in which the hair is further differentiated, but has not yet reached the surface.

Thus the more or less cylindrical hair-shaft consists of three parts—*medulla*, *cortex*, and *cuticle*: the medulla is the most important part of the hair, and on its structure mainly depend the differences seen in the hair of individual species.

The colour of the hair is due to three causes: firstly, to a greater or less accumulation of pigment in the cortical layer; secondly, to air contained in the intercellular spaces of the medulla; and lastly to the nature of the surface of the hair, *i.e.* whether it is rough or smooth.

The mode of formation of new hairs in post-embryonic stages is not thoroughly understood: when the hair is shed, it is not known whether the old papilla remains, or whether a new one is formed. The former method seems to occur in most instances, although not infrequently new hairs are formed throughout life direct from the epiderm, as in the embryo. From a primary hair-germ an entire group of hairs may be formed by subsequent division.

---

[1] This hair-rudiment at first more or less resembles the rudiment of an integumentary sense-organ of a Fish or gilled Amphibian; and this fact has led to the expression of a view that the origin of hairs may be traced phylogenetically to such sensory organs of the lower Vertebrates.

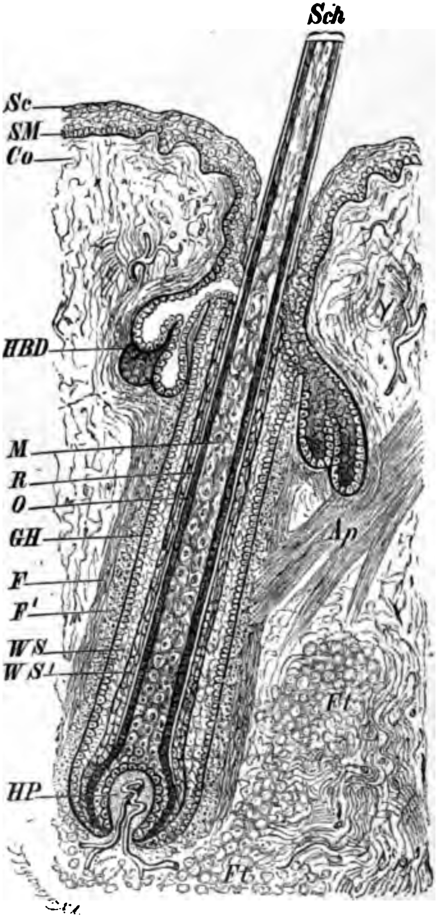

FIG. 23.—LONGITUDINAL SECTION THROUGH A HAIR. (Diagrammatic.)

Ap, arrectores pili; *Co*, derm; *F*, outer longitudinal layer, and *F'*, inner transverse layer of connective tissue fibres of follicle; *Ft*, adipose tissue; *GH*, hyaline layer, which lies between the inner and outer hair-sheaths, *i.e.*, between the root-sheath and the follicle; *HBD*, sebaceous glands; *HP*, hair-papilla, containing vessels; *M*, medulla; *O*, cuticle of shaft; *R*, cortex; *Sc*, stratum corneum; *Sch*, hair shaft; *SM*, stratum Malpighii; *WS*, *WS*¹, external and internal root-sheath—the latter reaches above only as far as the sebaceous ducts, and is not continuous with the epiderm.

The special tactile hairs (*vibrissæ, sinus-hairs*) present on parts of the face are usually much longer and stronger than the others, and are provided with striped muscle-fibres. They are the first to appear in the embryo, and the last to be retained in those forms which have lost their hairy covering in connection with an aquatic life (*e.g.* Cetacea). Between the outer and inner layers of their follicles are blood-spaces and cavernous tissue, and they are well supplied with branches of the trigeminal nerve. The ordinary hairs are also well innervated, especially in the case of nocturnal animals, and are sensory as well as protective in function. Other modifications of the hairs are seen, *e.g.* in the eye-lashes, the long tail-hairs of most Ungulates, and various other forms of bristles: *spines*, such as are characteristic of the Hedgehog and Porcupine, are merely especially strongly developed bristles.

Hairs, like feathers, are arranged in definite tracts (*flumina pilorum*), and the fur often consists of finer and coarser elements. A richer hairy covering (*lanugo*) is often met with in the embryonic condition than in the adult (*e.g.* in the human fœtus); and this fact, together with the occasional appearance of abnormally hairy individuals, indicates that at one time Man was distinguished by a far more abundant clothing of hair than at the present day.

Hairs are most scanty in the Cetacea and Sirenia, in the former of which they are often limited to a few bristles (sinus-hairs) in the region of the lips (Toothed Whales) or chin (Whalebone-Whales), or may be entirely wanting except in embryonic stages. In the Sirenia, apart from the persistent hairs, a thick coat of fine hairs is present in the embryo, and modified traces of these can be recognised in the epiderm of the adult.

The hairy coat may be shed and renewed periodically (*e.g.* in the case of Mammals exhibiting differences in their summer and winter fur), or the shedding and renewal may take place constantly, and so result in no marked change of coat.

Epidermic *scales* may also occur in Mammals, but are rarely present on parts which are well covered with hair. They are large and well marked in Manis, covering the dorsal surface of the head and body, the sides of the latter and the whole tail, and are present on the tail of various Rodents (*e.g.* Beaver, Anomalurus, Muridæ), Insectivores, Anteaters,[1] and Marsupials. Other epidermic structures formed as thickenings of the horny layer also play an important part in Mammals: such are, *claws*, *nails*, *hoofs*, the *horn-sheaths* of Ruminants, the so-called whalebone (*baleen*) of the Mystacoceti, the *palatal plates* of Sirenia, the thickened regions of the epiderm in Cetaceans and Pachyderms, the *ischial callosities* of certain Apes, and the *nasal horns* of the Rhinoceros, the last-mentioned of which consist of numerous hair-like horny fibres.

According to the form taken by the horny covering of the distal ends of the digits, the Mammalia may be subdivided into Unguiculata and Ungulata, the former group including those with claws or nails, and the latter those with hoofs. But no hard and fast line can be drawn between these structures, which in all cases are derivable from a simple form of claw, like that of Reptiles and Birds. The terminations of the digits are without a horny covering in Cetacea, though rudiments are present in the embryo of Toothed Whales; while among the Sirenia the Manatee possesses vestigial and variable nails.

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[1] Vestiges of horny scales also occur in Armadilloes.

The horny nail-plate is situated on the dorsal side of the digit, while ventrally is the softer *sole-horn*, which is continuous proximally with the pads or *tori* on which the foot partially or entirely rests when on the ground. The essential relations and chief modifications and reductions of these parts in various Mammals are illustrated in Fig. 24. Tori are present in most Mammals, and have a definite arrangement on the palms and soles (apical, interdigital, and proximal), and in them the dermal papillæ are either irregular or are definitely grouped, and may give rise to a series of concentric lines and arches.[1]

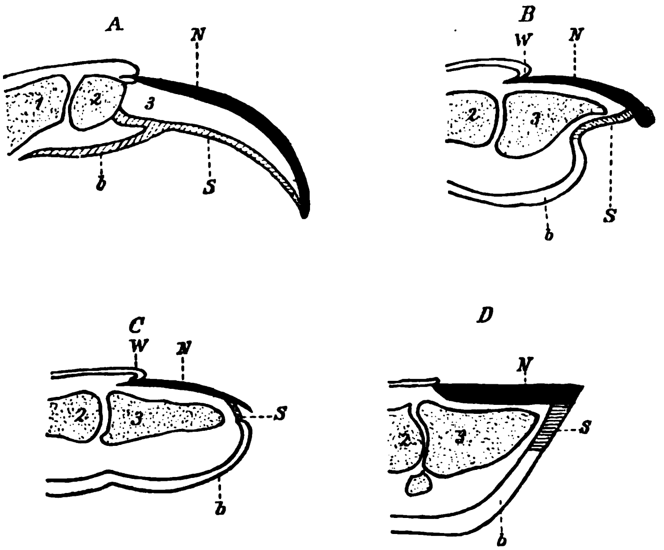

Fig. 24.—Diagrammatic Longitudinal Sections through the Distal Ends of the Digits of—*A*, Echidna; *B*, an Unguiculate Mammal; *C*, Man; and *D*, Horse (after Gegenbaur and Boas).

1—3, phalanges; *b*, torus; *N*, nail-plate; *S*, sole-horn; *W*, bed of claw or nail.

When pigment is present (*e.g.* on the snout, external genitals, and teats), it is chiefly situated in cells of the Malpighian layer into which it wanders from the derm, which may also contain pigment.

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[1] Compare those of Man, which yield the characteristic "finger-prints."

In the derm, as may be seen by a glance at Fig. 25, an outer papillary and an inner reticular portion may be distinguished. The papillæ of the former are accurately adapted to the over-lying epiderm: some of them contain blood- and lymph-capillaries, and others, nerves with tactile corpuscles. The latter, on the other hand, becomes lost without any sharp boundary line in the subdermal connective tissue and in the more or less well-developed fatty layer (*panniculus adiposus*). The panniculus may be very largely developed in aquatic Mammals—*e.g.* in the Cetacea, in which it serves to preserve the heat of the body, and at the same time to reduce the specific gravity of the animal.

As in Birds, the connective tissue fibres of the derm are irregularly felted. Most of the smooth muscle-fibres are inserted into the hair-follicles (*arrectores pilorum*, Fig. 23), but may occur independently of hairs, *e.g.*, in the scrotum and teats.

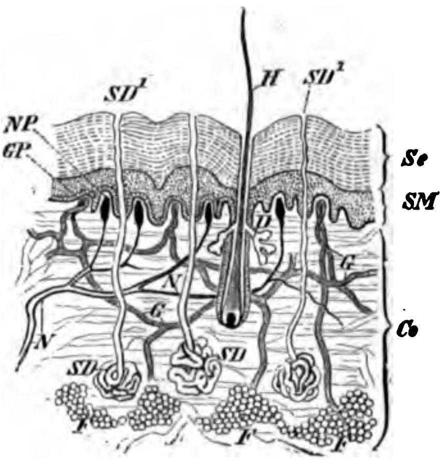

FIG. 25.—SECTION THROUGH THE HUMAN SKIN.

Co, derm; *F*, subcutaneous fat; *GP*, vascular papillæ; *H*, hair with sebaceous glands (*D*); *N* and *G*, nerves; *NP*, sensory-papillæ; *Sc*, stratum corneum; *SD*, sweat-glands, with their ducts (*SD*¹); *SM*, stratum Malpighii.

In the great abundance of integumentary glands, Mammals differ greatly from Reptiles and Birds, and more nearly resemble Amphibians. They may be present in all parts of the skin, and differ greatly with regard to the consistency, composition, colour, and odour of their secretions. Those which serve for the excretion of products of destructive metabolism in general, and for the formation of odoriferous substances, are either tubular or alveolar in structure. The former, which were probably derived from those of ancestral Amphibians, possess a muscular investment, have mostly the form of the characteristically coiled *sweat-glands*, and are rarely entirely wanting (*e.g.* Cetacea): the latter, which are a new acquisition and are known as *sebaceous glands*, appear to be not only functionally, but also ontogenetically and phylogenetically closely connected with the hairs (Figs. 23 and 25). Various modifications of both kinds are met with, and they are often arranged in groups. Thus the nasolabial glands of cattle, the lateral glands of the Shrew, and the dorsal glands of Hyrax resemble sweat-glands; while the preputial and Meibomian glands, the inguinal glands of certain Rodents, and the facial glands of Bats, are largely, at any rate, modified sebaceous glands.[1]

Another important modification of the integumentary glands is seen in the characteristic *mammary glands*, to the possession of which the Class owes its name, and which secrete milk for the nourishment of the young. Nothing is known of their phylogeny in the ancestors of Mammals, but in all cases they correspond to

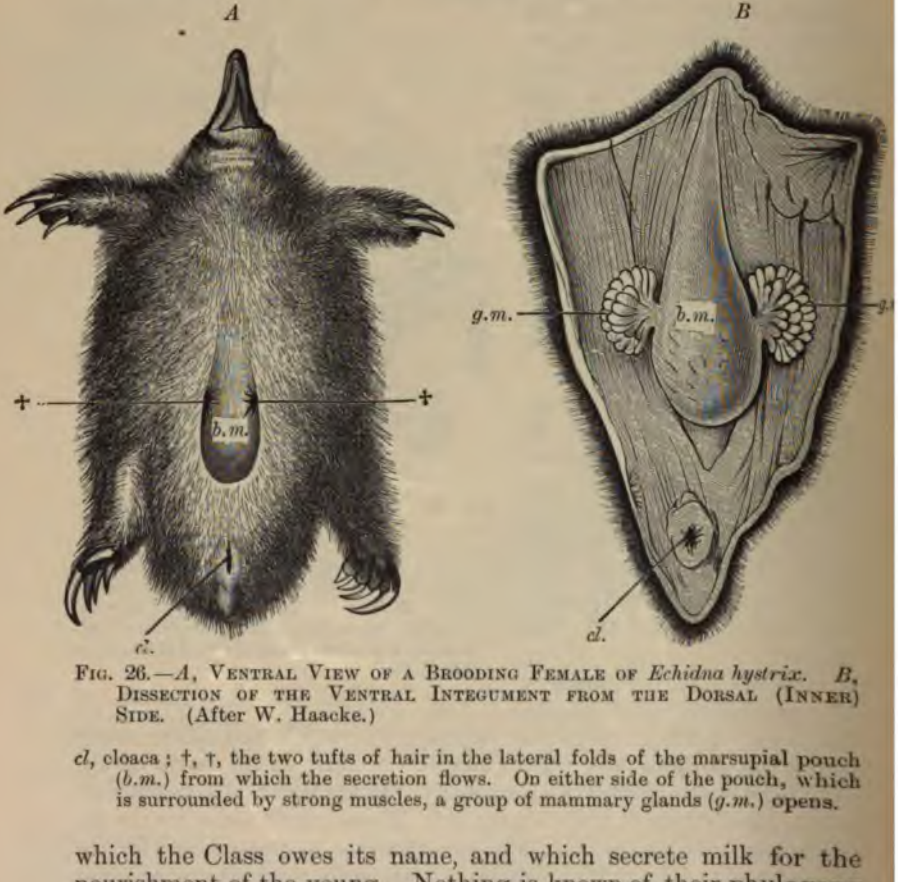

FIG. 26.—*A*, VENTRAL VIEW OF A BROODING FEMALE OF *Echidna hystrix*. *B*, DISSECTION OF THE VENTRAL INTEGUMENT FROM THE DORSAL (INNER) SIDE. (After W. Haacke.)

cl, cloaca; †, †, the two tufts of hair in the lateral folds of the marsupial pouch (*b.m.*) from which the secretion flows. On either side of the pouch, which is surrounded by strong muscles, a group of mammary glands (*g.m.*) opens.

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[1] Amongst many other modifications of these glands of both types may be mentioned the anal glands (especially well developed, *e.g.*, in Manis and the Skunk); the perineal or prescrotal glands of Viverra; the caudal gland of the Fox and Wolf; the suborbital or antorbital glands situated in the cavity of the lacrymal bone in Cervidæ; and the interdigital glands of many Ruminants. The preputial glands of the Beaver and Musk-deer also deserve special mention.

A peculiar tubular, femoral or spur-gland is present at the knee in Echidna and dorsal to the hip-joint in Ornithorhynchus, near the vertebral column. It opens by means of a long duct on to the tarsal spur, and, though present in the *embryo of both* sexes, undergoes reduction in the female.

modified integumentary glands which have a certain similarity to sweat glands, and like these, are probably specialised forms of primitive tubular glands. The sebaceous glands arise much later ontogenetically, but it is interesting to note that in the development of the mammary area, traces of early stages of hairs may be observed: these disappear later, but their sebaceous glands become connected with the mammary ducts.

Potentially, therefore, mammary organs may be developed in any part of the skin, but as a matter of fact, they are limited to the ventral side in adaptation to the method of suckling the young.

Amongst the oviparous Monotremes, a *marsupial pouch* appears in the embryo of Echidna as an infolding of the abdominal wall (Fig. 26). This pouch, which serves to shelter the egg and young, becomes temporarily enlarged in the breeding season as the offspring increases in size, and has the form of a deep sac extending backwards and provided with closing muscles. On its lateral walls are a pair of depressions, the so-called *mammary pockets*, which also arise periodically. A bunch of hairs is present in each pocket, the follicles of which open along with the mammary ducts on these two glandular areas, which are sharply marked off from the rest of the pouch. The mammary glands themselves, which are almost equally developed in the two sexes, consist in Echidna of long, coiled, and much branched tubes, the blind ends of which are swollen. Both they and the mammary pockets are acted upon by a strong integumentary compressor muscle, the presence of which is all the more necessary as Monotremes possess no teats. The manner in which the young take in the milk is uncertain: it has been supposed that the milk drops from the two bunches of hairs and is then licked off; or it may be that a temporary teat is formed by suction.[1]

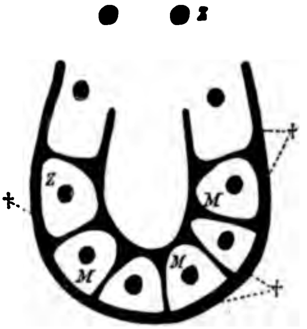

FIG. 27.—RUDIMENT OF THE MARSUPIUM IN *Didelphys marsupialis*, RECONSTRUCTED FROM TRANSVERSE SECTIONS. (After Bresslau.)

M, marsupial pockets; *Z*, teats or mammary pockets; †, lateral walls of the marsupial pockets which fuse to form the walls of the pouch.

Amongst Marsupials, in which *teats* are present, the pouch is evidently homologous with that of Echidna, but it reaches a higher stage of development. A solid ring-like ridge of the epiderm is formed around each teat (or mammary pocket from which the teat arises), and later on the areas thus enclosed sink inwards so as to give rise to a row of hollows or *marsupial pockets*, which together constitute what has been called the *marsupial line* (Fig. 27). By a fusion of the adjacent lateral walls of the pockets arise the marsupial folds which form the pouch (Fig. 28). The lowest Marsupials show no trace of a pouch, and their ancestors probably never possessed one.

---

[1] Nothing definite is known as to the manner in which Ornithorhynchus cares for its young. The eggs are laid in burrows in the earth, and it appears that no marsupial pouch is formed at any time; possibly it may have gradually disappeared as the animal acquired an aquatic habit. The sieve-like apertures of the mammary gland are distributed over two spindle-shaped areas on the ventral body-wall which are covered by the fur and surrounded by integumentary muscles.

Marsupial pockets persist permanently in various degrees of perfection in a number of the Eutheria (*e.g.* Manidæ, Muridæ, Cervidæ, Carnivora). In Mice they can be recognised until the beginning of lactation, and are then evaginated and thus lengthen the teats.

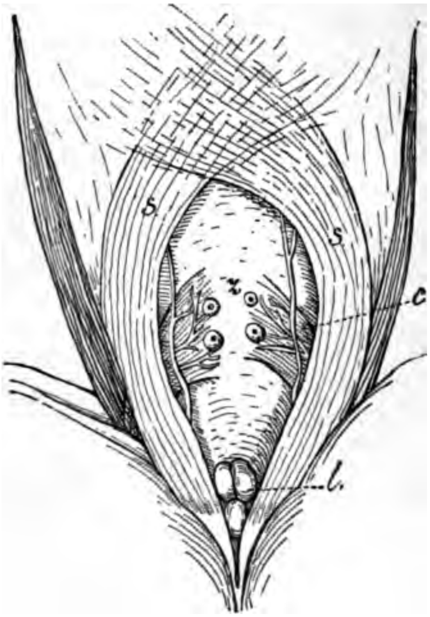

Fig. 28.—Pouch of *Thylacinus*, after Removal of the Skin. (After Cunningham.)

c, compressor mammæ (=cremaster of male), passing over which are seen blood-vessels and the genito-crural nerve; *l*, lymphatic glands; *s*, sphincter marsupii; *z*, teats.

The teats may become developed in one of two ways. Either the skin surrounding the mammary pocket (Fig. 29, A) becomes raised up to form a circular rampart, and thus gives rise to a teat perforated by a canal, into the base of which the ducts of the gland open (B); or the gland surface itself becomes elevated into a papilla, while the surrounding skin remains almost on a level with the rest of the integument (C). In the latter case, therefore, there is an evagination of the mammary pocket, and the teats may be described as *secondary* or *true* (Marsupials, Rodents, Lemurs, Monkeys, and Man), and in the former as *primary* or *pseudo-teats* (Carnivores, Pigs, Horses, and Ruminants). The latter condition is already indicated in certain Marsupials (*e.g.* Phalangista vulpina).

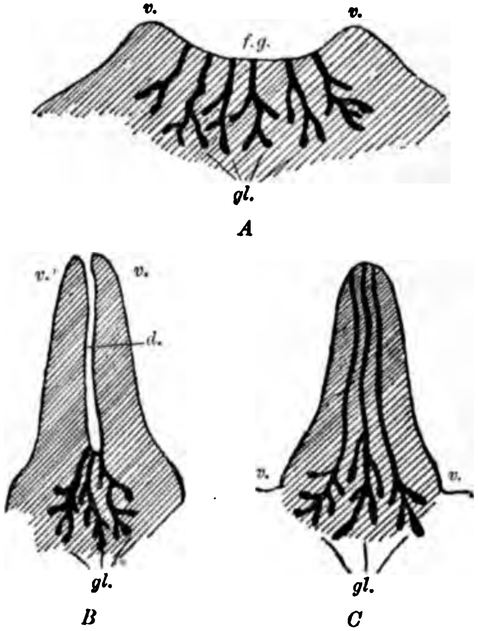

FIG. 29.—DIAGRAMMATIC REPRESENTATIONS OF THE EARLY DEVELOPMENT OF THE LEADING TYPES OF MAMMARY GLANDS. (Modified from Gegenbaur.)

A, first or undifferentiated (mammary pocket) stage; *B*, stage of the pseudo- (primary) teat; *C*, stage of the true (secondary) teat; *d*, mammary canal; *f.g*, glandular area; *gl*, mammary glands; *v*, rim (or rampart) of the glandular area.

The teats are often situated in two nearly parallel rows along the ventral side of the thorax and abdomen which slightly converge towards the inguinal region (*e.g.* Carnivores, Pigs): in other cases they may be restricted either to the inguinal (Ungulates and Cetaceans) or to the thoracic region (Sloths, Manis, Elephants, Sirenia, many Lemurs, Cheiroptera, and Primates): while in others, again, they may be axillary or abdominal, or they may occur in various combinations of all these regions.

The number of teats varies greatly: there may be as few as one pair, or as many as eleven pairs (Centetes): in general, their number corresponds to that of the young produced at one birth.

Not infrequently, supernumerary or accessory mammæ and teats can be recognised (*e.g.* in Sheep and Cattle), and there may be indications in the fœtus of a greater number of teats than that which occurs in the adult: thus in the embryo of Whalebone-Whales there are eight pairs, while the adult possesses only a single pair on either side of the vulva. Cases of such a *hypermastism* and *hyperthelism* are also well known in the human subject, as frequently in men as in women. The accessory mammæ and teats are usually anterior (above) or posterior to (below) the normal ones, and thus form with them two converging rows from the axillary to the inguinal region, just as in many other Mammals and in the human embryo, at a certain stage of which four pairs of additional rudiments of mammary organs can always be recognised. There is thus an indication of normal hypermastism and hyperthelism in human ontogeny, which is paralleled in those numerous mammals in which a "*mammary ridge*" or "*line*" is formed, a structure which is probably comparable to the "*marsupial line*" forming the rudiment of the pouch in Marsupials.

In the male, the mammary apparatus becomes absorbed, though frequently at birth and at puberty milk is produced in the human subject. Male goats and castrated sheep have also been known to give milk.

B. SKELETON.

1. EXOSKELETON.

THE hard exoskeleton, consisting of bone or of other calcified tissues, must be distinguished from the horny exoskeletal parts already described. Thus it will be remembered that the term "scale" is sometimes used for a horny epidermal structure, and sometimes for a bony dermal one (pp. 20 and 23).

In **Cyclostomes,** scales are entirely wanting.

Elasmobranchs.—The integument of most Elasmobranch Fishes encloses certain hard structures each consisting of a *basal plate* or socket bearing a pointed spine or *denticle* (Fig. 30), differing considerably in form and relative size in the various members of the Order, and known as a *placoid scale.* These placoid organs are continually being formed anew throughout life, and are protective in function. The basal plate is rhomboid or rounded in form and consists of bony tissue, while the denticle itself is composed of *dentine* covered over with *enamel.* In many Rays, there is a relatively small number of these placoids, while in most Sharks and Dogfishes they are much more numerous and close-set. In the Electric Rays they are wanting. The primary part

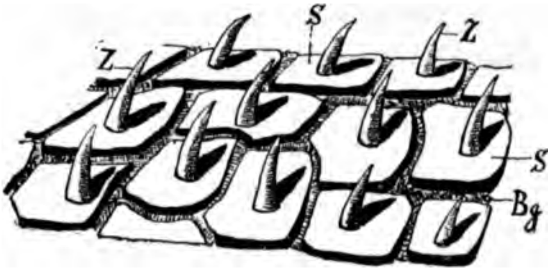

FIG. 30.—PLACOID SCALES FROM THE SKIN OF AN ELASMOBRANCH. (Semi-diagrammatic.)

S, basal or socket-plates in the dermal connective tissue (*Bg*); *Z*, denticles.

is the enamel, which is formed as an excretion of the epidermic cells (Fig. 31), while the later formed mesodermal dentinal and bony portions become closely connected with the enamel secondarily. Thus the enamel is the first and originally the only hard substance of the placoid organ.

In the Holocephali (Chimæra, Callorhynchus) a double row of placoids is developed along parts of the dorsal region in the embryo, but disappear in later stages: in the adult these organs apart from the spine on the anterior margin of the dorsal fin, occur only on the claspers and frontal organ of the male.[1]

Teleostomes.—In these Fishes, ossifications in the derm to form bony scales takes place independently of any stimulus from the epiderm. Thus the denticle, which in Elasmobranchs is the primary cause of the development of the basal plate, gradually disappears in ontogeny, and the latter is the only part of the placoid organ which remains, its independence being retained in the formation of bony skeletal substance in higher Vertebrates.

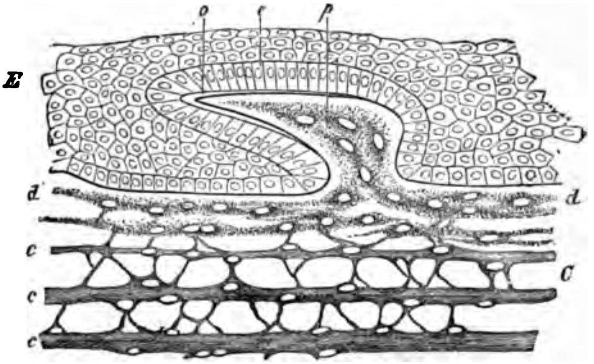

Fig. 31.—Vertical Section through the Skin of an Embryo Shark. (From Gegenbaur's *Comp. Anatomy.*)

C, derm; *c*, *c*, *c*, *d*, layers of the derm; *E*, epiderm; *e*, its layer of columnar cells; *o*, enamel layer; *p*, dermal papilla.

In Lepidosteus, denticles are still developed in the skin but are quite transitory, and this primitive method of starting the formation of bony tissue is again met with in the Vertebrate series in connection with certain parts of the Amphibian skull; here certain bones (vomer, palatine, pterygoid, &c.) which originally served as supports for oral teeth, persist even if the teeth disappear, as they have become an integral part of the facial skeleton.

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[1] In addition to the ordinary placoid scales, larger or smaller spines of a similar structure may become developed in connection with the dorsal fin, around the first cartilaginous ray (*e.g.* Acanthias, Trygon, Chimæra). In the Sawfish (Pristis), there is a double row of large denticles on the long rostrum.

It is therefore evident that the first bony hard substances of the Vertebrata arise in connection with the external skin and oral mucous membrane, and that the bony integumentary skeleton, or *exoskeleton*, is therefore phylogenetically older than the bony internal skeleton or *endoskeleton*. The latter owes its origin to a gradual extension of the exoskeleton from the surface to deeper parts, where it takes on relations to the cartilaginous endoskeleton. An independent ossification of the perichondrium, or membrane which invests the cartilage, may also take place, so that bone and cartilage now combine in the formation of the skeletal framework and thus further complications arise. To the original dermal ossification is added a formation of bone in the perichondrium, and finally even a secondary endochondral ossification may occur, replacing the cartilage: the former is most marked in the Anamnia, the latter in the Amniota, and the result of both is usually the subjection of the cartilaginous tissue in the struggle of the tissues in the organism.

In most *Ganoids*, thick plates, usually rhombic in form, are present in the skin; in the bony Ganoids (Polypterus, Lepidosteus)[1] these cover the entire body, their margins being in apposition. These *ganoid scales* correspond to the deeper part of the placoid basal plates. Their surface is dense and smooth, owing to the presence of a layer of *ganoin*, of mesodermal origin, and formerly erroneously described as enamel. The exoskeleton was largely developed amongst fossil Ganoids.

The scales of *Teleosts* are usually thin, and of the form known as *cycloid* or *ctenoid;* in the former the whole margin is smooth, while in the latter the posterior margin is toothed and comb-like, but various intermediate stages occur. The scales are arranged in oblique rows and are situated directly beneath the epiderm, the individual scales not touching one another. Secondarily, they usually come to lie within definite pockets or sacs, and to overlap one another like tiles on a roof (Figs. 13 and 32). The surface of the scales may be sculptured.

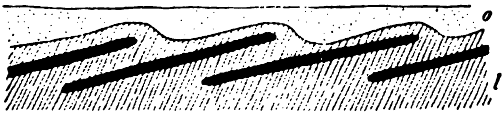

FIG. 32.—DIAGRAMMATIC LONGITUDINAL SECTION THROUGH THE SKIN OF A TELEOSTEAN, TO SHOW THE RELATION OF THE BONY SCALES. (From Boas's *Zoology.*)

l, derm; *o*, epiderm; *s*, scale.

In the developing scale, a superficial dense portion, formed from cells and corresponding to the dentinal layer of the basal plate, can be distinguished from a deeper part composed of several layers of connective tissue: each of these becomes independently ossified in a typical manner.

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[1] In Amia the scales have a "cycloid" form, and in the adult Polyodon they are absent.

Numerous other forms of the dermal skeleton are met with in Teleosts. In some of these Fishes (*e.g.* Plectognathi, Lophobranchii, certain Siluroids),[1] as in many of the earliest Palæozoic Vertebrates (Ostracodermi), bony scutes are developed and form a strong cuirass. In others, again (*e.g.* many Siluroids and Eels), the scales may be reduced or absent. The bony dermal fin-rays or "leptotrichia" of Teleostomes possibly correspond to modified scales.

Dipnoans.—In the Dipnoi, as in the Teleostomi, the scales are not directly derivable from the Elasmobranch placoids. In form, in their overlapping arrangement, and in their situation in pockets of the derm, they resemble the cycloid scales of Teleosts; but this similarity must have come about independently in the two cases, that is, must be due to convergence.

Amphibians.—Recent Amphibians have retained only very slight traces of such a dense integumentary bony armour as was present in the fossil Stegocephali. Amongst these, specially strong dermal plates were formed in the region of the shoulder-girdle, and very commonly most of the body was covered with scales. A series of oblique and bilaterally symmetrical rows of scales covered the entire ventral surface between the shoulder- and hip-girdles, a further differentiation of which results in the scales no longer overlapping, but forming short parallel rods, which correspond to the so-called "abdominal ribs" ("parasternal elements") of certain Reptiles. As examples of exoskeletal structures in existing forms may be mentioned the bony plates in the skin of the back of certain Anura (Ceratophrys dorsata and Brachycephalus ephippium), as well as the scales lying between the ring-like folds of the limbless Amphibia (Gymnophiona). The latter resemble in many respects the scales of Fishes, and may be derived from such a scaly covering as that of the Permian Salamander Discosaurus.

Reptiles.—The dermal skeleton was very highly developed amongst fossil Reptiles, *e.g.* certain Dinosaurs, such as the Jurassic Stegosauridæ, in which enormous bony plates and spines covered with horn, sometimes as much as sixty-three centimetres long, were present in the dorsal region. Teleosaurus and Aëtosaurus (Crocodilia), as well as some of the gigantic Cretaceous Dinosaurs, (Ceratopsidæ), possessed a strong exoskeleton.

Amongst existing Reptiles a series of well-developed "abdominal ribs" (cf. p. 42) are present in Hatteria in the rectus abdominis muscle, each consisting of a median and of a paired lateral bar, and being considerably more numerous than the body metameres. In Crocodiles similar bars are present, their number corresponding with that of the ribs: they no longer reach the middle line, and with the exception of the first, each consists, on either side, of two firmly united portions. Evidently these structures have here begun to undergo reduction.

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[1] In these Siluroids, the bony plates may bear sockets in which denticles, consisting of dentine and enamel, are implanted. But although denticles are retained in these cases, they do not contribute to the formation of the basal plates, as in Elasmobranchs.

Crocodiles, many Lizards (Anguis, Cyclodus, Scincus), and more especially Chelonians, exhibit a well-developed dermal skeleton, the scutes composing which cover the body more or less completely. In the last-mentioned group there is a dorsal and ventral shield (*carapace* and *plastron*) consisting of numerous more or less closely united pieces, and completely encircling the body (Fig. 33). The plastron, the larger posterior portion of which probably corresponds to greatly modified abdominal ribs, arises entirely by ossification of the derm; while parts of the carapace have a close relation to the endoskeleton (neural arches and ribs), which early in development became broadened out into plates. At the same time, the intercostal muscles disappear completely, and the muscles of the back undergo partial reduction, while the articulations of the vertebræ and ribs disappear. The nuchal, pygal, and marginal plates (cf. Fig. 33) are entirely independent of the endoskeleton—that is, are purely exoskeletal bones; while the costal and neural plates correspond to much thickened periosteal bones developed around the cartilaginous ribs and neural spines respectively: though they are subcutaneous in position, they have nothing to do with the skin genetically.

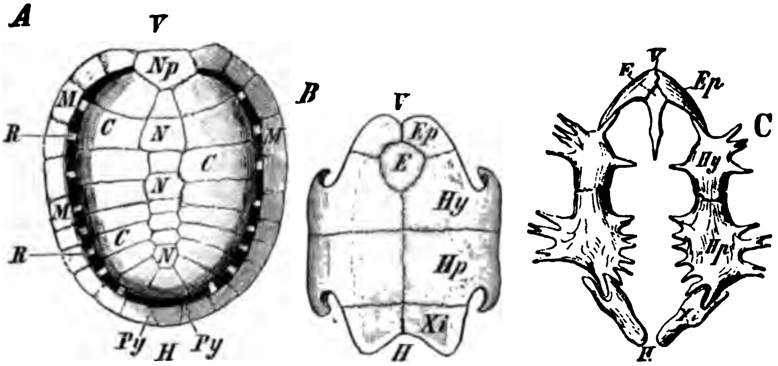

FIG. 33.—*A*, CARAPACE, and *B*, PLASTRON OF A YOUNG *Testudo græca*; *C*, PLASTRON OF *Chelone midas*.

C, costal plates; *E*, entoplastron; *Ep*, epiplastron; *Hp*, hypoplastron; *Hy*, hyoplastron; *M*, marginal plates; *N*, neural plates; *Np*, nuchal plate; *Py*, pygal plates; *R*, ribs; *Xi*, xiphiplastron. (*V* indicates the anterior, and *H* the posterior margin.)

Reference has already been made to the dermal bones amongst fossil Fishes, Amphibians, and Reptiles, and certain of these in the antero-ventral region of the trunk are of special interest, as they are represented in certain Reptiles by a bone known as the *episternum*, which underlies the sternum. Though always arising as a paired structure, the episternum, which is present, *e.g.*, in Palæohatteria, most Lizards (Fig. 56) and Crocodiles, forms in the adult an unpaired plate of varied form. It is wanting in Chamæleo, Anguis, Ophidia, and Chelonia.[1]

Birds.—Reduced abdominal ribs occur in the primitive Archæopteryx, otherwise no fossil or existing Birds possess a dermal exoskeleton, and no independent elements corresponding to an episternum can be recognised even in the embryo: they have evidently long ago disappeared.

Mammals.[2]—Armadillos are the only Mammals possessing a bony exoskeleton,[3] which consists of a series of five movable transverse bony scutes covering the head, neck, and body, and of smaller plates on the tail and limbs. Sparse hairs occur between these plates. It is very doubtful whether this exoskeleton has been derived from that of Reptiles: more probably it, like the horny exoskeleton of Manis (p. 31), has arisen secondarily, and in consequence of its development the hairs have become reduced. In Glyptodon, a large fossil member of this group, the dermal plates were firmly united together to form a shield which covered the whole body.

2. ENDOSKELETON.

Under the term exoskeleton are included the bony parts which, as a rule, remain throughout life in connection with the integument: the *endoskeleton* consists mainly of cartilaginous and bony parts, all of which have a deeper position. The cartilaginous portions, which in their entirety constitute the *primordial endoskeleton*, have undoubtedly from the first arisen in this position, and for a long period formed, together with the notochord, the entire internal skeleton, as they practically do at the present day in Elasmobranchs as well as in Cyclostomes. As already mentioned (p. 41), bone may be developed in connection with this primordial skeleton and may arise in two different ways. It may be formed in parts which are not superficial; or bony elements may become associated with the cartilaginous skeleton which are derived phylogenetically from the exoskeleton but which in course of time have taken up a deeper position: these become secondarily connected with the bones which have arisen independently in this position. In order to determine as to which of these two categories any particular bone belongs, an appeal to comparative Embryology is necessary.

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[1] Unless the element of the plastron marked *E* in Fig. 33 is to be interpreted as such.

[2] A certain part of the anterior end of the sternum, as well as certain cartilaginous and bony elements in the region of the sterno-clavicular articulation, are sometimes said to correspond to the last remains of the dermal episternum of lower forms; but as further proofs are required before such a homology can be definitely accepted, the term *prosternum* has been proposed to include the elements in question (cf. under Sternum).

[3] It is possible that the peculiar horny tubercle in the region of the dorsal fin in certain Cetaceans may represent the last vestiges of a dermal bony armature such as was present in the extinct Zeuglodon.

The relations of a bone to the cartilaginous skeleton may be of such a nature that it merely becomes applied to the outside of the cartilage, when it may be described as an *investing bone.* A bone may, however, originate in the perichondrium or membrane which covers the cartilage, and then, in the course of phylogenetic development, may invade and replace the cartilage: in other words, *perichondral* bone may become *endochondral.*[1] The cartilage beneath investing bones may gradually disappear in the course of time, and occasionally a bone which was originally perichondral may attain apparent independence by the loss of the cartilage around which it was formed in the first instance.

I. VERTEBRAL COLUMN.

An elastic rod, the *notochord,* or *chorda dorsalis,* lying in the longitudinal axis of the embryo between the neural and visceral tubes (cf. p. 6), is the first part of the endoskeleton to be formed, and is the primitive forerunner of the vertebral column. It is developed as a ridge of the primary endoderm, from which it becomes constricted off, and is therefore of epithelial origin. In the large parenchyma-like cells of which it is composed vacuoles soon appear, and eventually only the walls of the cells persist in the greater part of the notochord; these become flattened by mutual pressure, so that they appear like a meshwork of pith-cells (Fig. 34, A, B). At the periphery, however, the cells retain their protoplasm, becoming flattened and arranged like an epithelium. Around the notochord two homogeneous, cuticular sheaths are successively developed from its cells. The *primary sheath* is first secreted by the peripheral notochordal cells: the thicker *secondary sheath,* which has a similar origin from the so-called "notochordal epithelium," appears later.

From the surrounding mesoderm a *skeletogenous layer* is developed: this not only surrounds the notochord, but extends dorsally to it as well as ventrally. Thus a continuous tube of embryonic connective tissue is formed enclosing the spinal cord,

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[1] The unsatisfactory terms "membrane-bones" and "cartilage" bones are usually used in describing the investing and replacing bones.

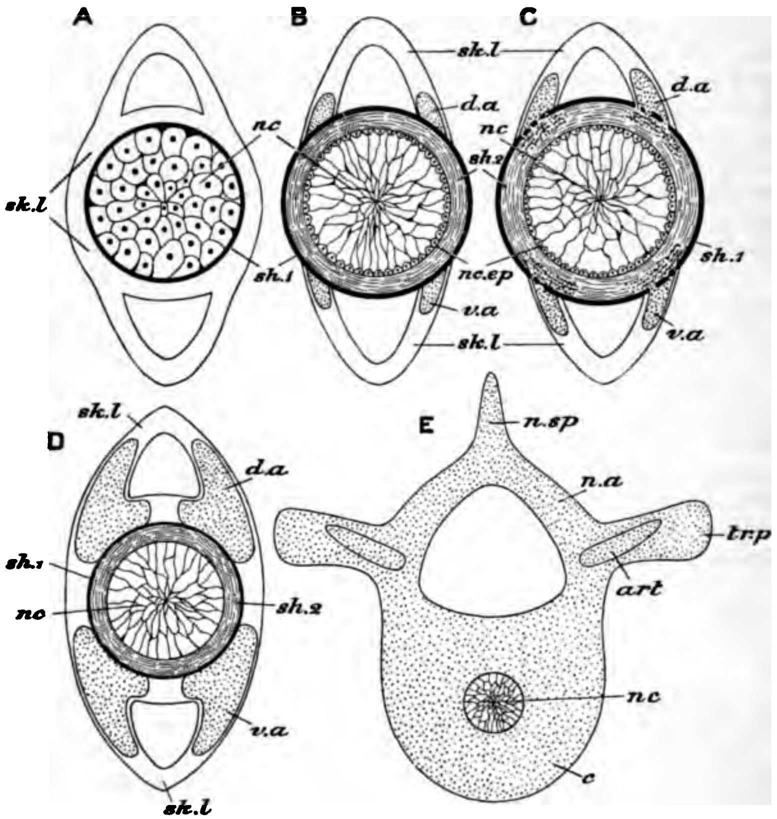

FIG. 34.—DIAGRAMS ILLUSTRATING THE DEVELOPMENT OF THE NOTOCHORDAL SHEATHS AND VERTEBRAL COLUMN.

A.—Early stage, showing notochordal cells (*nc*) and primary sheath (sh^1), as well as the mesodermic skeletogenous layer (*sk.l*).

B.—Later stage, in which the central notochordal cells (*nc*) have become vacuolated, and the peripheral cells have given rise to the "notochordal epithelium" (*nc. ep.*) from which the secondary sheath (sh^2) is derived: paired dorsal and ventral cartilages, or arcualia (*d.a*, *v.a*) have arisen in the skeletogenous layer (Cyclostomes, Cartilaginous Ganoids).

C.—Cartilage cells have passed through the primary sheath, and are invading the secondary sheath (Elasmobranchii, Dipnoi).

D.—The cartilages are growing round the notochord, outside its sheaths, which gradually become reduced (Bony Ganoids, Teleostei, Amphibia, Amniota).

(*A*—*D* represent the caudal region.)

E.—A later stage in the development of a pre-caudal vertebra. The notochord (*nc*) has become constricted, and the cartilages have united into a single mass and have given rise to a centrum (*c*), neural arch (*n.a*), neural spine (*n.sp*), transverse processes (*tr.p*), and articular processes (*art*).

and only broken through at the points of exit of the spinal nerves. This stage is often known as the *membranous stage*, and in it no indication is seen of the metameric segmentation which occurs later in the vertebral axis. The cause of this segmentation is to be traced primarily to the muscular system; and it is evident, on mechanical grounds, that the segmentation of the vertebral column must alternate with that of the muscular segments or myotomes. Small paired and segmentally arranged masses of cartilage later appear in the skeletogenous tissue dorsally and ventrally to the notochord, and these represent the rudiments of the *vertebræ* (Fig. 34, B, E). This is the beginning of the second or *cartilaginous stage* of the vertebral column; and now ossification may occur (*bony stage*). Those parts of the fibrous tissue which do not become consolidated in this manner give rise to the *ligaments* of the vertebral column.

Two different modes of development of the vertebral column from the above-mentioned dorsal and ventral cartilages or *arcualia* may be observed. In Elasmobranchs and Dipnoans the secondary notochordal sheath undergoes a fibrillar degeneration, and becomes invaded by cartilage-cells from the arcualia which break through the primary sheath at these points (Fig. 34, C) and gradually extend so as to surround the notochord, thus forming a cartilaginous sheath which may undergo segmentation to form a series of vertebral bodies or *centra*; the arcualia at the same time extend dorsally and ventrally respectively to form the vertebral (*neural* and *hæmal*) *arches*. In other cases (*e.g.* Bony Ganoids, Teleosts, Amphibians, and Amniota), the arcualia extend at their bases round the notochord so as completely to surround it without penetrating the primary and secondary sheaths (D). The centra which are then formed by segmentation of this perichordal cartilage may be described as *perichordal centra*, to distinguish them from the *chordal centra* of Elasmobranchs and Dipnoans.

During these differentiations of the skeletogenous tissue, the notochord suffers a very different fate in the various Vertebrate groups; it may increase in size and persist as a regular cylindrical rod, or it may become metamerically constricted by the formation of the vertebral bodies, and even entirely disappear. In all Vertebrates above Elasmobranchs, the embryonic vertebral column is relatively shorter than the notochord around which it is formed, and thus there has been a phylogenetic reduction in length of the axial skeleton.[1]

Amphioxus.—The notochord of Amphioxus exhibits many primitive as well as special characters. It extends along the whole length of the animal, whereas in the Craniata it always ends anteriorly below the brain just behind the pituitary body.

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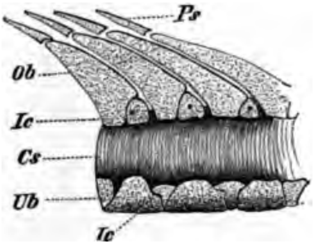
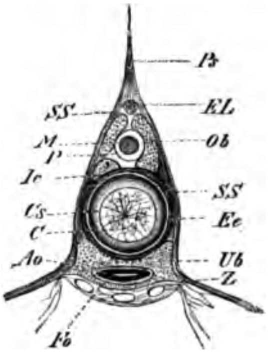
[1] An ephemeral structure, the *subnotochordal rod* or *hypochorda*, occurring in embryos of Fishes and Amphibians, may be briefly referred to in this place. It arises as a longitudinal furrow or ridge of the endoderm in the head and trunk, on the dorsal side of the gut, with which it may for a time remain in connection, but eventually becomes constricted off as a rod lying beneath the notochord. It soon undergoes degeneration, but traces of it may persist as an elastic band. It seems probable that this structure is a vestige of the epipharyngeal groove of Amphioxus.

A delicate primary sheath is present and is surrounded by connective tissue which is continuous with that enclosing the neural canal and separating the muscular segments or myotomes.

Cyclostomes.—In these, as in all the true Fishes, only two regions can be distinguished in the vertebral axis, a *trunk-* or *precaudal region*, and a *caudal region*. An advance on the primitive condition in Amphioxus is seen in the development of a thick secondary sheath and, at any rate in the caudal region, of cartilaginous elements: in the adult Petromyzon these are present all along the notochord in the form of rudimentary neural arches, which, however, do not meet above the spinal cord (cf. Fig. 34, B), and of which there are two pairs to each muscular segment or myotome (cf. Elasmobranchs). In the tail hæmal arches, enclosing the caudal aorta and vein, are also present, and fusion of the cartilaginous elements occurs.





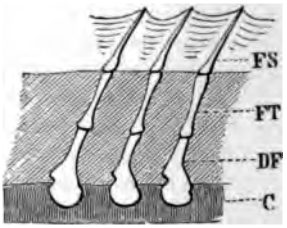


FIG. 35.—PORTION OF THE VERTEBRAL COLUMN OF *Polyodon*. Side view.

FIG. 36.—TRANSVERSE SECTION OF THE VERTEBRAL COLUMN OF *Acipenser ruthenus* (in the anterior part of the body).

Ao, aorta; *C*, notochord; *Ee*, primary, and *Cs*, secondary sheath of the notochord; *EL*, longitudinal elastic band; *Fo*, median ingrowths of the lower arches enclosing the aorta ventrally; *Ic*, intercalary pieces (inter-dorsal and inter-ventral); *M*, spinal cord; *Ob*, upper arch (basi-dorsal); *P*, pia mater; *Ps*, neural spine; *SS*, skeletogenous layer; *Ub*, lower arch (basi-ventral; *Z*, "basal stumps" of the lower arches.

FIG. 37.—PORTION OF THE VERTEBRAL COLUMN OF *Protopterus*. Side view. *C*, notochord; *DF*, neural spine; *FS*, fin-ray; *FT*, interspinous bone.

Fishes.—To the condition found in Cyclostomes, that seen in the *Cartilaginous Ganoids*, *Holocephali*, and *Dipnoi*, is directly comparable: the notochord is persistent, no centra being formed, as was also the case in the most primitive Palæozoic Elasmobranchs, and thus the metameric character of the skeletal axis is only seen in the arches (Figs. 35, 36, and 37). In the Holocephali and Dipnoi, however, the thick secondary sheath encloses cartilage cells amongst its fibres. In Chimæra narrow calcified rings are also developed in the sheath: these are considerably more numerous than the arches. The latter remain cartilaginous in the Cartilaginous Ganoids and Holocephali, but become densely ossified in the Dipnoi (Fig. 37). The upper arches may be completed above by *neural spines.* In the caudal region the hæmal arches usually enclose the caudal aorta and vein completely; further forwards the cartilages do not meet in the middle line below, thus only surrounding the cœlome to a slight extent, and consequently the lower arches end on either side in a laterally-directed cartilaginous projection, the *transverse process* or "*basal stump.*"

The relations of the arches in *Plagiostomes*, *Bony Ganoids*, and *Teleosts* are similar to those described above, but their structure is more complicated in all Fishes than is there indicated.

The upper arches, which in many Fishes are not closed in dorsally,[1] consist on either side of several distinct elements, which are most plainly distinguishable in Cartilaginous Fishes. One of these (directly above the centrum where such is developed) may be described as the *basidorsal* or *neural plate*, and is usually perforated by the foramen for the motor root of a spinal nerve. Intercalated between successive basidorsals is another cartilage, the *interdorsal* (*intercalary piece*, or *interneural plate*), through which the sensory root of a spinal nerve, situated anteriorly to the corresponding dorsal root, usually passes: both these cartilages may meet above, so as to complete the arch (Fig. 38). In some cases, more than one intercalary piece is present on either side, and frequently another series of cartilages becomes segmented off from the basidorsals and interdorsals respectively to form the keystone of the arch: these give rise in the median line to more or less marked *neural spines.* The bases of this series of upper intercalary pieces or *supradorsals* fit in alternately between the

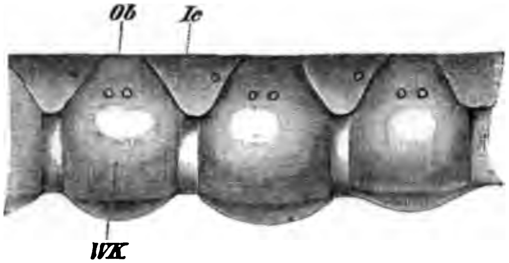


FIG. 38.—PORTION OF THE VERTEBRAL COLUMN OF *Scymnus*.

Ic, intercalary pieces (interdorsals); *Ob*, neural arches (basidorsals); *WK*, centra. The apertures for the roots of spinal nerves are shown.

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[1] A longitudinal elastic ligament is constantly present in this region (Figs. 36 and 42) and also in relation with the ventral arches.

basidorsals and interdorsals, and thus may be twice as numerous as the centra (Fig. 39).[1] The lower arches consist of *basiventral* cartilages, between which are sometimes intercalated a series of *interventrals* (Fig. 35), and which, in the tail, are produced into *hæmal spines:* these may be formed of distinct *infraventral* elements.

In *Dipnoans* the interdorsals and interventrals are fused or wanting, and in Bony Ganoids and Teleosts the various elements usually become united in the fully-formed vertebra. Distinct fused pairs of supradorsals, however, persist and remain unossified in Lepidosteus (Fig. 42), and in the caudal region of Amia the basidorsals and basiventrals remain separate from the interdorsals and interventrals, thus giving rise to double vertebral bodies (*precentra*, bearing the arches, and archless *postcentra*). A somewhat similar condition is seen in the Jurassic Eurycormus and other fossil Ganoids. From what has been said above, it will be seen that the number of arch elements does not necessarily correspond

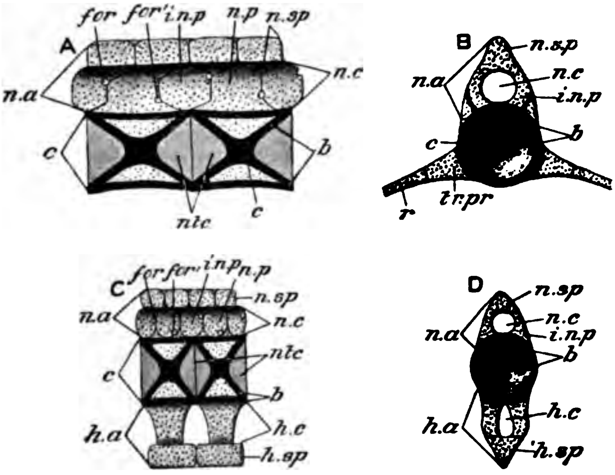

FIG. 39.—PORTIONS OF THE VERTEBRAL COLUMN OF *Scyllium canicula*. (From Parker's *Practical Zoology*.)

A and *B*, from the trunk; *C* and *D*, from the middle of the tail; *A* and *C*, two vertebræ in longitudinal section; *B* and *D*, single vertebræ viewed from one end; *b*, calcified portion of centrum; *c*, centrum; *for*, foramen for dorsal, and *for'*, for ventral root of spinal nerve; *h.a*, hæmal arch (basi-ventral); *h.c*, hæmal canal; *h.sp*, hæmal spine; *i.n.p*, intercalary piece (interdorsal, or interneural plate); *n.a*, neural arch; *n.c*, neural canal; *n.p*, neural plate (basi-dorsal); *n.sp*, neural spine; *ntc*, intervertebral substance (remains of notochord); *r*, proximal portion of rib; *tr.pr*, transverse process (basal stump).

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[1] It was mentioned on p. 48 that in the Lamprey there are two pairs of arcualia to each myotome: it is possible that they correspond to alternating basidorsals and interdorsals.

with that of the centra, or the number of the latter with that of the myotomes.

Articular processes (*zygapophyses*) are usually present on the neural arches of Bony Fishes.

In *Plagiostomes*, the cartilage which has invaded the sheath of the notochord is segmented into definite vertebral centra, which become partially calcified in various ways. The calcification (Fig. 40) may in each centrum take the form of a double cone, constricted in the middle, as in Scymnus and Acanthias (*cyclospondylic* form); concentric layers may be added to this, as in the Rays (*tectospondylic*); or longitudinal plates may be formed radiating outwards from the double cone, as in Scyllium (*asterospondylic*). The dorsal and ventral arches usually extend round the centrum so as to enclose it, and in the tail there may be two or more sets of vertebral elements to each body segment.[1]

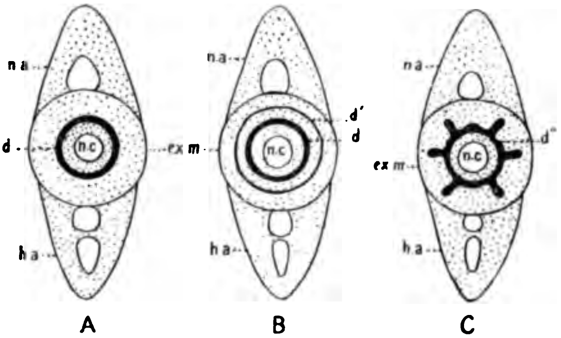

FIG. 40.—DIAGRAMMATIC TRANSVERSE SECTION THROUGH THE MIDDLE OF A CYCLOSPONDYLIC (A), A TECTOSPONDYLIC (B), AND AN ASTEROSPONDYLIC VERTEBRA (C). (From Zittel, after Hasse.)

d, middle portion of the calcified double cone; *d'*, additional concentric calcified layers; *d''*, double cone with radiating calcified layers; *ex.m*, external elastic membrane; *h.a*, hæmal arch; *n.a*, neural arch; *n.c*, notochordal cavity.

In *Bony Ganoids* and *Teleosts*, there is a tendency towards a reduction of the cartilage; that which forms the centra is entirely outside the notochordal sheaths, and the vertebræ become more or less densely ossified.

In the course of development of the centra in all cases, the notochord becomes constricted by the growth of the cartilage at regular intervals while the latter undergoes segmentation into centra. Each point of constriction corresponds to the middle of a centrum, *i.e.*, it is intravertebral in position, and the notochord may here disappear entirely; intervertebrally it remains expanded and so persists as a kind of connecting or packing substance between contiguous centra, which are consequently of a deeply *biconcave* or *amphicœlous* form (Fig. 41).

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[1] In Rays and Chimæroids the anterior vertebral elements become fused into a single mass, on which a definite condyle is formed for articulation with the skull; amongst Sharks and in Dipnoans also, a concrescence of the anterior vertebral elements with one another and with the skull may occur.

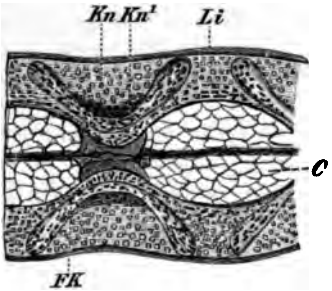

Fig. 41.—Portion of the Vertebral Column of a Young Dogfish (*Scyllium canicula*). (After Cartier.)

C, notochord; *FK*, the fibro-cartilaginous mass lying between the cartilaginous zones which is undergoing calcification; *Kn*, outer, and *Kn'*, inner, zone of cartilage; *Li*, invertebral ligament.

One of the Bony Ganoids, Lepidosteus, forms a marked exception to other Fishes as regards its vertebral column, inasmuch as definite articulations are formed between the centra (Fig. 42). A concavity is formed at the hinder end of each centrum which articulates with a convexity on the vertebra next behind (*opisthocœlous form*). The notochord (except in the caudal region) entirely disappears in the adult; in the larva it is seen to be expanded intravertebrally and constricted intervertebrally, a condition of things which appears again in the higher types, as, for instance, in Reptiles. In a still earlier larval stage, however, the constrictions are intravertebral, as in other Fishes.

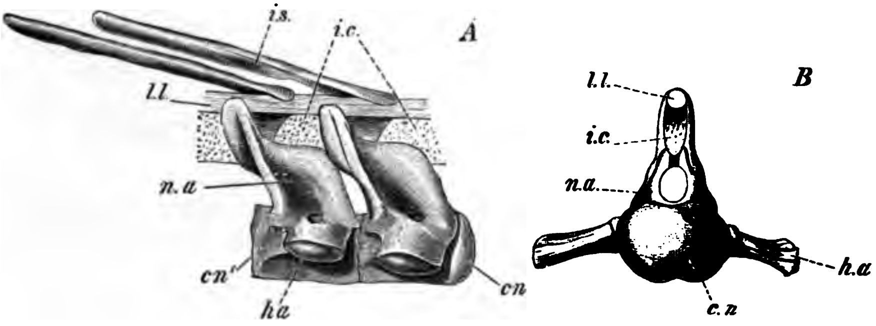

Fig. 42.—Portion of the Vertebral Column of *Lepidosteus*. (After Balfour and Parker.)

A, vertebra from anterior surface; *B*, two vertebræ from the side. *cn*, anterior convex face, and *cn'*, posterior concave face of centrum; *h.a*, transverse process; *i.c*, intercalary cartilages (fused supra-interdorsals); *i.s*, interspinous bone; *l*, *l*, longitudinal ligament; *n.a*, upper arch (basi-dorsal).

The skeleton of the posterior end of the tail in Fishes requires special notice, and the condition in Amphioxus, Cyclostomes, and Dipnoans, may be taken as a starting-point. In these, the notochord extends straight backwards to the hinder end of the body and is surrounded quite symmetrically by the tail-fin, and the tail is therefore spoken of as *diphycercal*: this condition is also met with in certain Palæozoic Fishes. In most other Fishes the ventral part of the tail-fin with its supporting skeleton, as a result of unequal growth, is more strongly developed than the dorsal part, and the vertebral column becomes bent up dorsally, giving rise to a *heterocercal* tail. This form of tail may be recognised externally in most Elasmobranchs, Ganoids, and numerous fossil Fishes, or may be masked by a more or less symmetrical tail-fin, as in Lepidosteus, Amia, and more particularly in most Teleosts, in which the heterocercal character is only visible internally, and the tail is described as *homocercal* (cf. Figs. 43, *A* and *B*). The posterior end of the vertebral column is then frequently represented by a rod-like *urostyle*, and in Teleosts one or more wedge-shaped *hypural bones* (enlarged hæmal arches) generally occur directly beneath it.[1]

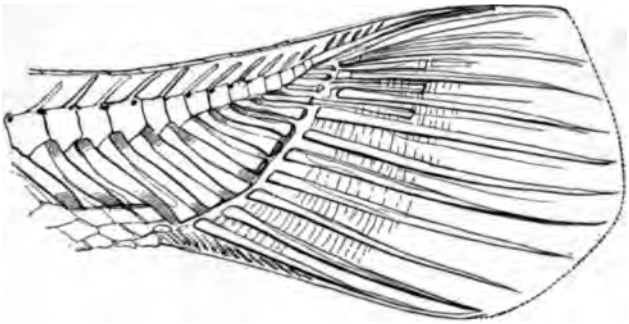

FIG. 43A.—TAIL OF *Lepidosteus*.

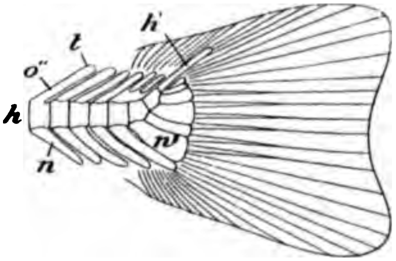

FIG. 43B.—CAUDAL END OF VERTEBRAL COLUMN OF SALMON. (From Boas's *Zoology*.)

h, centrum ; *h'*, urostyle ; *n*, hæmal arch ; *n'*, hypural bone ; *o''*, neural arch ; *t*, neural spine.

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[1] The diphycercal character of the tail in Dipnoi and certain Teleostomi is probably not primitive (*protocercal*), but has been acquired secondarily.

As a rule Elasmobranchs and Ganoids possess a greater number of vertebræ (up to nearly 400) than Teleosts, in which we seldom meet with more than 70: the Eel, however, possesses more than 200, while amongst the Plectognathi there may be as few as 15.

The tendency towards a fusion of the various components such as occurs in the ossified vertebræ of Bony Ganoids and Teleosts is also seen in the Amphibia and Amniota, the notochord being of less importance and the vertebræ becoming more consolidated and secondarily modified in various directions. Thus the homology of the different elements of which they are composed can only be traced by a study of their development; but even in the adult, parts are frequently present which recall the primarily composite nature of the vertebræ, as will be seen in the following pages.

Amphibians.—Amongst Amphibians, the vertebral column is more or less distinctly differentiated into *cervical*, *thoraco-lumbar*, *sacral*, and *caudal* regions, and these regions can be recognised, except in certain modified types, in all the higher Vertebrates. On account of the absence of extremities in Cæcilians, there is no sacral region, and in Anura, the caudal portion is modified to form a urostyle (Fig. 45).

The notochord of Urodele larvæ, like that of most Fishes, undergoes intravertebral constrictions, while intervertebrally it remains thicker, and accordingly appears expanded. Thus the centra here also are *amphicœlous*. In the course of their development, a gradual reduction of the cartilage may be observed, and the bone, originally perichondral in origin, becomes correspondingly independent (Fig. 44). The cartilage is more and more limited on the one hand to the arches (Fig. 52), and on the other to the intervertebral regions round the notochord, extending to a greater or less degree into the anterior and posterior ends of the individual bony vertebral bodies, thus constricting or even entirely obliterating the notochord in these regions. The bony centra are formed from the bases of the arches, which, before ossification, only rest on the notochord and do not enclose it. Finally a differentiation, as well as a resorption, extending inwards from the periphery, occurs in these cartilaginous parts: in the interior of each an *articular cavity* is formed, so that in the vertebræ of many higher Urodeles an anterior convexity and a posterior concavity may be distinguished, both covered with cartilage; they are, therefore, *opisthocœlous* (Fig. 44).

In the development of the vertebral column of Urodeles we can thus distinguish three stages:—(1) A connection of the individual vertebræ by means of the intervertebrally expanded notochord; (2) a connection by means of intervertebral masses of cartilage; and finally (3) an articular connection. These three different stages of development find a complete parallel in the phylogeny of tailed Amphibians, inasmuch as many of the Stegocephali of the Carboniferous period, as well as the Perennibranchiata, Derotremata, and many Myctodera, possess simple biconcave bony centra without differentiation of definite articulations.[1]

Thus the bony parts of the vertebræ of Urodeles are not formed from the cartilage surrounding the notochord, but in connective tissue, there being only an intervertebral cartilaginous zone, extending into the ends of the centra. In the Anura, on the

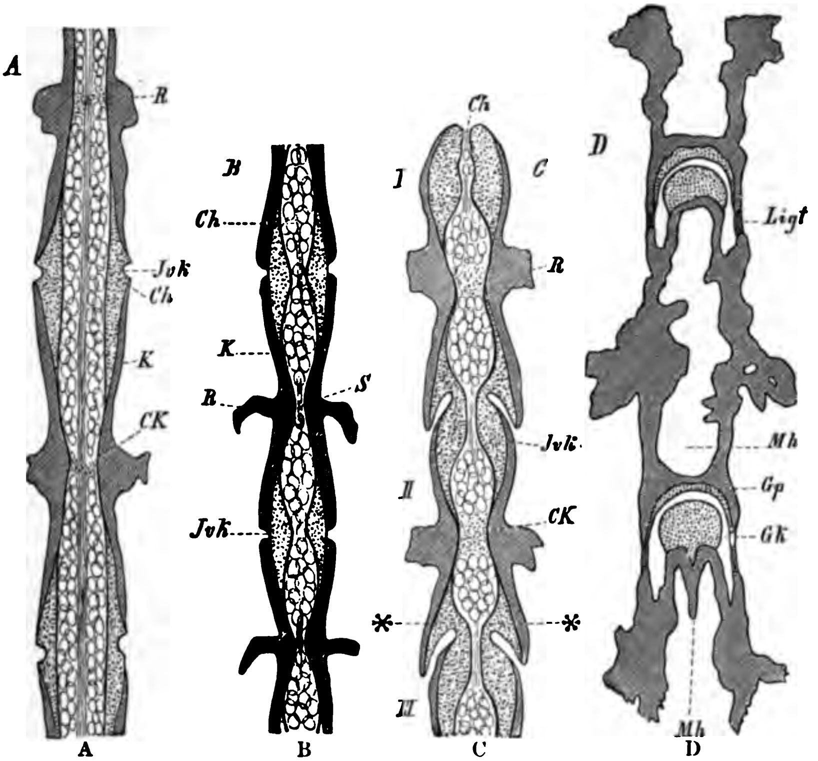

FIG. 44.—LONGITUDINAL SECTION THROUGH THE VERTEBRAL CENTRA of VARIOUS URODELES. A, *Ranodon sibericus*; B, *Amblystoma tigrinum*; C, *Gyrinophilus porphyriticus* (*I*, *II*, *III*, the three anterior vertebræ); D, *Salamandrina perspicillata*.

Ch, notochord; *CK*, intravertebral cartilage and fat-cells; *Gp*, concave posterior face, and *Gk*, convex anterior face of centrum with articular socket and head; *Jvk*, invertebral cartilage; *K*, superficial bone of centrum; *Ligt*, intervertebral ligament; *Mh*, marrow cavity; *R*, transverse process; *S*, intravertebral constriction of notochord in *Amblystoma*, without cartilage and fat-cells; **, intervertebral cartilage.

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[1] In certain of the Stegocephali incomplete hoops of bone, the *intercentra*, and *pleurocentra*, twice as numerous as the arches, surrounded the persistent notochord (cf. the caudal region in Amia and Elasmobranchs, p. 50).

other hand, as in Elasmobranchs, Teleosts, Bony Ganoids, and the higher Vertebrates, the vertebræ are preformed in cartilage, and true articulations are always formed between them: as a rule, but by no means always, the convexity is posterior and the concavity anterior (*procœlous* form). A further difference is seen in the relations of the notochord, which persists intravertebrally longer than intervertebrally, in this respect resembling Lepidosteus and Reptiles.

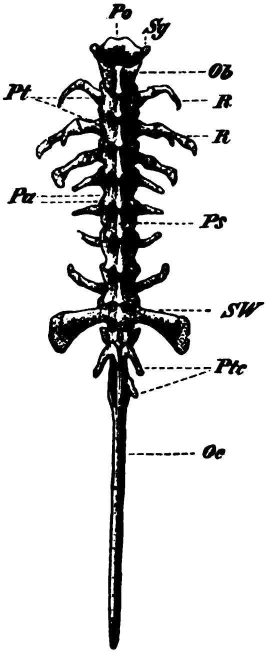

FIG. 45. — VERTEBRAL COLUMN OF *Discoglossus pictus.*

Ob, upper arch of first vertebra; *Pa*, articular processes; *Po*, anterior process of first vertebra; *Ps*, neural spine; *Pt*, transverse processes of trunk vertebræ; *Ptc*, tranverse processes of caudal vertebræ (urostyle, *Oc*); *R*, ribs; *Sy*, condylar facets of first vertebra; *SW*, sacral vertebra.

The configuration of the caudal region of the vertebral column must also be remarked upon, as it differs in tailed and tailless Amphibians. The long caudal portion of the vertebral column in Anuran larvæ, which is very similar to that of Urodeles, undergoes during metamorphosis a gradual retrogressive modification, and the vertebræ of its proximal end become fused and co-ossified to form a long, unsegmented, dagger-like bone, the *urostyle* (Fig. 45).

Hæmal arches are present in the caudal region of Urodeles only. The neural spines, as well as the transverse processes, which in Urodeles are as a rule bifurcated at the base and are present from the second vertebra onwards, show the greatest variety as regards shape and size, differing in the several regions of the body. The transverse processes of the single *sacral vertebra*, which give attachment to the pelvis, are particularly strongly developed, especially in the Anura (Fig. 45), in which the number of presacral vertebræ is usually only eight.

Articular processes (*zygapophyses*) are well developed in all Vertebrates from Urodeles onwards, and consist of two pairs of projections arising from the anterior and posterior edges respectively of the neural arch. Their surfaces are covered with cartilage and overlap one another from vertebra to vertebra, and in some Urodeles the neural spines also articulate with one another: thus a well-articulated and mobile, chain-like vertebral column results.

The first or *cervical* vertebra becomes differentiated from the others, and consists of a comparatively simple ring which articulates by means of lateral facets with the two condyles of the skull, and also, in Urodeles, with the base of the latter by means of a projection, of varying size and form, the so-called "odontoid" process; thus a freer movement between the skull and vertebral column is rendered possible. This vertebra, however, is not homologous with the first vertebra (*i.e.* the atlas) of the higher Vertebrates, as is demonstrated by a study of its development, which shows that the real atlas, with the exception of the part which forms the "odontoid," loses its individuality as a separate mass, and becomes united with the occipital region of the skull.

The number of vertebræ present in Urodeles is inconstant, and varies greatly: it may reach to nearly 100 (Siren), and in Cæcilians may be very much greater (up to 275).

Reptiles.—In many fossil Reptiles (Theromorpha, Ichthyosauria, &c.) the centra were biconcave, and this primitive form, with an intervertebrally expanded notochord, is retained in the Ascalabota amongst existing forms: the Rhynchocephali also possess amphicœlous vertebræ, but intercentral fibro-cartilaginous discs occur in their existing representative, Hatteria. A primitive character of the Rhynchocephalian vertebral column is seen in the retention throughout of the primary components of the centra as distinct elements, wedge-shaped *intercentra* being intercalated between the centra proper or *pleurocentra*: in the majority of Lacertilia intercentra also occur, but are usually only recognisable in the neck and tail; in Chelonians a few intercentra are present in the neck region. A pair of elements interposed between the upper part of the first vertebra (atlas) and the skull in Crocodiles, usually known as the "pro-atlas" (Fig. 46), which is represented also in Hatteria, Chameleons, and many fossil forms, corresponds to a disconnected pair of "supra-dorsal" elements (p. 49).

In the majority of Reptiles, the notochord remains expanded longer in the intravertebral regions than intervertebrally, but in the adult it becomes entirely aborted and replaced by bony tissue. This stronger and more solid ossification of the whole skeleton forms a characteristic difference between the Ichthyopsida on the one hand and the Amniota on the other. As a rule the centra of Reptiles are of the procœlous type and become definitely articulated with one another: the forms with intervertebral remains of the notochord and those with fibro-cartilaginous *intervertebral discs*, (*e.g.* Crocodiles) form an exception to this rule. In Crocodiles the vertebræ are mostly procœlous, an exception being seen in the two sacrals and first caudal. In Chelonians there is great variation in the form of the individual centra of the cervical vertebræ—even in the same individual procœlous, opisthocœlous, biconcave, and even biconvex centra, with intervertebral discs, may occur; while the thoracic and lumbar vertebræ have flattened faces, and are firmly united with one another by cartilage, and also with the carapace (p. 43).

What has been said as to the classification of the vertebræ into different regions in Urodeles, as well as to the presence of the various processes, usually applies here also to a still greater extent. Except in limbless form, there are always several cervical vertebræ instead of a single one, and also typically at least two sacral vertebræ. The two first cervical vertebræ become differentiated to form an *atlas*—bearing a single occipital facet and usually formed of three pieces, and an *axis*—with an odontoid bone belonging morphologically to the centrum of the atlas (cf. p. 57).

The neural spines vary in size, and transverse processes arise from the centra themselves or close to them. Lower arches, or *chevron bones*, corresponding to the intercentra, are present in the tail in Lizards, Crocodiles, and some Chelonians; and besides these, median inferior processes of the centra themselves are seen in many of the vertebræ of Lizards, Crocodiles, and Snakes: in the last mentioned paired processes partly enclose the caudal vessels. The arches in Snakes, Lizards, and usually in Chelonians, become united with the centra by synostosis, while in Crocodiles they remain, at any rate for a long time, separated from them by sutures (Fig. 46).

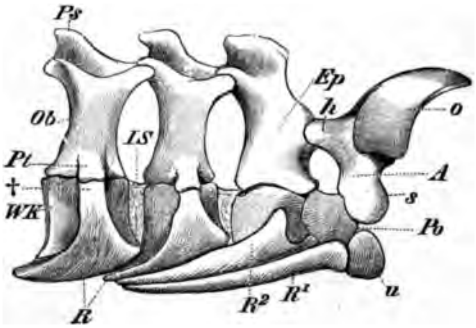

Fig. 46.—Anterior Portion of the Vertebral Column of a Young Crocodile.

A, atlas; *Ep*, axis, articulating with the atlas at *h*; *Is*, intervertebral disc; *o*, "pro-atlas"; *Ob*, neural arch; *Po*, odontoid bone; *Ps*, neural spine; *Pt*, transverse process, arising from the base of the arch and articulating with the rib at †; R^1, R^2, *R*, ribs; *u*, ventral element, and *s*, arch of atlas; *WK*, centrum.

In Snakes, Hatteria, and some Lizards (Iguana) extra articular processes (*zygosphenes* and *zygantra*) are developed on the neural arches; and in the caudal region of Hatteria and Lizards an unossified septum remains in the middle of each centrum (which really corresponds to two primary vertebral elements), so that the tail easily breaks off at these points. When this happens the tail grows again, but true vertebræ are not formed.

The greatest number of vertebræ is seen in Snakes, in which there may be over 400.

Birds.—The vertebral column of Birds has many points of resemblance with that of Reptiles both phylogenetically and ontogenetically. In both groups the notochord usually eventually disappears entirely, and the whole skeleton becomes strongly ossified. Archæopteryx, as well as the Cretaceous Ichthyornis, possessed biconcave vertebræ, but in existing adult Birds this character never occurs except in the free caudal vertebræ. Cervical, thoracic, lumbar, sacral, and caudal regions can be distinguished. The arches always become united into a single mass with the corresponding centra, not remaining separated from them by sutures, as is the case in certain Reptiles: even the ligament which keeps the odontoid process of the axis in its place may become ossified. Fibro-cartilaginous discs or menisci, perforated in the centre by a ligament, are present between the centra.

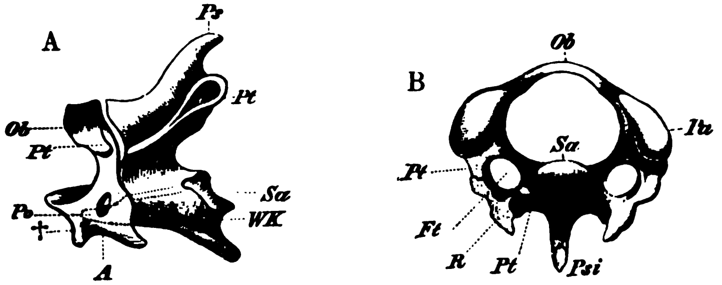

FIG. 47, A.—ATLAS AND AXIS (from the left side), and B, THIRD CERVICAL VERTEBRA (ANTERIOR FACE) OF WOODPECKER (*Picus viridis*).

A, *Ob*, *A*, arch and centrum of atlas; *Po*, odontoid process; *Ps*, neural spine of axis; *Pt*, transverse process; *WK*, centrum of axis, and *Sa*, its saddle-shaped articular surface for the third vertebra; †, condylar facet.

B, *Ft*, vertebrarterial foramen; *Ob*, neural arch; *Pa*, articular process; *Pt*, *Pt*, the two bars of the transverse process, shown on one side ankylosed with the cervical rib (*R*); *Psi*, median inferior process (hypapophysis).

In the cervical region, which is extremely flexible and often very long, the centra are in nearly all cases connected by means of saddle-shaped (*heterocœlous*) synovial articulations; the upper part of each bifurcated transverse process arises from the arch, the lower from the centrum, and these may unite with the corresponding forked rib, the vertebral artery and vein extending through the foramen thus formed (Fig. 47). The ring-like atlas, with its single facet for the occipital condyle, is relatively small, and the odontoid is fused with the axis. In the thoracic and lumbar regions more or fewer of the vertebræ usually become immovably united together.

The sacral region in Bird-embryos, like that in existing adult Reptiles, consists of two vertebræ only, the transverse processes of which ossify separately and correspond to fused ribs, as in Amphibia and Amniota. During further development, however, a number of other (*secondary* sacral) vertebræ (thoracic, lumbar, and caudal), with their rudimentary ribs, become fused with the two *primary* ones (Fig. 48), so that the entire number of vertebræ in the sacrum may be as many as twenty-three. In Archæopteryx the sacrum was much shorter than in existing Birds, and fewer vertebræ were united with it.

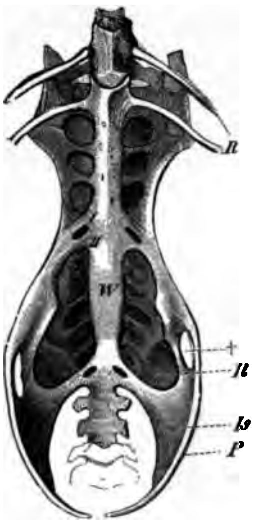

FIG. 48.—PELVIS OF OWL (*Strix bubo*). Ventral view.

Il, ilium; *Is*, ischium; *P*, pubis; *R*, last two pairs of ribs; *W*, position of the primary sacral vertebræ: between *R* and *Il*, and behind *W*, are seen the secondary sacral vertebræ, fused with the primary (*W*); † foramen between ilium and pubis.

In existing Birds the actual caudal region always exhibits a more or less rudimentary character, and in its posterior portion the vertebræ usually fuse together to form a flattened bone, the ***pygostyle***, which supports the tail quills (Fig. 132). In the Ratitæ there is never more than an insignificant pygostyle (Struthio), and all the caudal vertebræ may remain distinct. That the latter is the more original condition in Birds is shown by a study of their development as well as by the condition of the tail in Archæopteryx, in which it was supported by numerous elongated free vertebræ (Fig. 49). It must, however, be borne in mind that the pygostyle may be made up of from six to ten fused vertebræ, and in the sacrum even a greater number may be included, so that as many as twenty or more caudal vertebræ may be represented.

Mammals.—The notochord here persists longer intervertebrally than intravertebrally, but it disappears entirely by the time the adult condition is reached. A jelly-like pulpy mass, the ***nucleus pulposus***, persists, however, throughout life in the centre of the fibro-cartilaginous menisci which are developed between the centra. The whole vertebral column is preformed in cartilage, and the arches develop in continuity with the centra but become ossified from separate centres, as do also the various processes; these separate ossifications are no longer recognisable in the adult. The presence of bony discs or *epiphyses* on the flattened ends of the centra which unite with the latter comparatively late, is very characteristic of Mammals; they are, however, absent or only imperfectly developed in Monotremes and in existing Sirenians.

True articulations between the centra are usually only formed on the atlas and anterior face of the axis; well-developed articular processes (zygapophyses) are present on the neural arches.[1] The cervical region is usually the most movable, and the centra may here possess articulations and have an opisthocœlous form

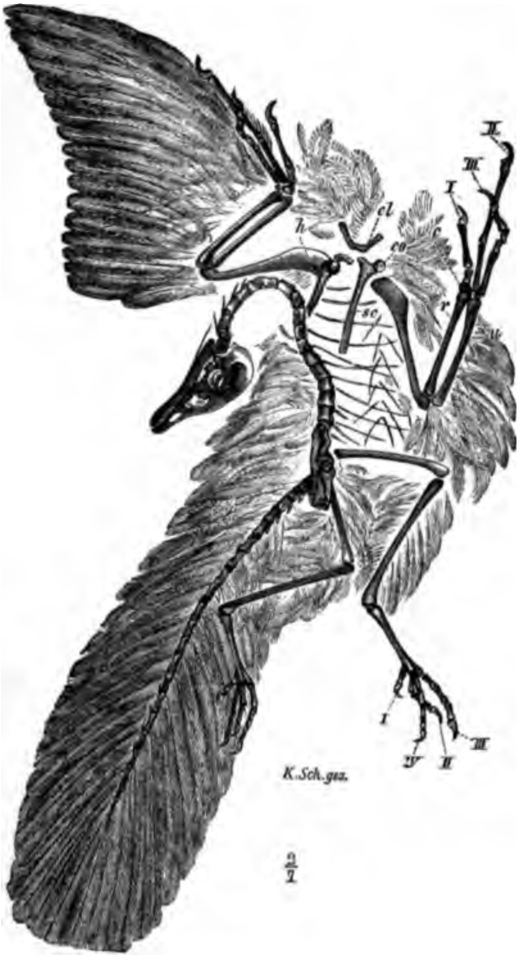

Fig. 49.—*Archæopteryx lithographica.* From the Solenhofen slates (Jurassic). After Dames, from the specimen in the Berlin Museum.

c, carpus; *cl*, clavicle; *co*, coracoid; *h*, humerus; *r*, radius; *sc*, scapula; *u*, ulna; *I—III*, digits of manus; *I—IV*, digits of pes.

(Ungulata). In some cases, on the other hand, the cervical vertebræ may become firmly fused with one another (*e.g.* Dasypus, Talpa, Cetacea).

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[1] In certain Edentata (*e.g.* Myrmecophaga, Dasypus) extra articular processes are present besides the ordinary zygapophyses on the posterior thoracic and lumbar vertebræ.

The atlas[1] and axis essentially resemble those of Birds, except that the condylar facet on the former is paired; in many Marsupials the ventral part of the axis may consist merely of a fibrous band. The differentiation of the vertebral column into regions characterised by difference of form is much more sharply marked than in any other Vertebrates. There are as a rule seven cervical vertebræ; amongst the Edentata, however, Bradypus possesses eight to nine, and Tamandua bivittata, eight, while in Cholœpus (and also in the Manatee) there are only six.

The transverse processes are simple except in the cervical region and arise from the base of the arch. In the neck, they are united with the vestiges of the cervical ribs, and in nearly all cases enclose a vertebrarterial canal, as in Birds (p. 59): in Monotremes these rib-vestiges remain distinct at any rate for a long time. In the thoracic region the transverse processes are tipped with cartilage on the ventral side of their distal ends for articulation with the tubercle of the rib (*q.v.*). In the lumbar and sacral regions they arise from the centra, and contain fused rib-elements.

The number of thoraco-lumbar vertebræ varies greatly in different Mammals; there may be as few as fourteen (Armadillo) or as many as thirty (Hyrax). In Ungulates the number is constantly nineteen. In the lumbar vertebræ the transverse processes are especially long, and other processes (anapophyses, metapophyses, hypapophyses) may be characteristically present in this region.

Thus, as in Amphibians, Reptiles and Birds, the pelvis is connected with the sacrum by means of vestigial ribs. As in the two last-mentioned groups, there are not more than two primary sacral vertebræ, but except in Ornithorhynchus and most Marsupials a few caudal vertebræ become later included in the sacrum and are usually more or less closely united with it by synostosis. The various processes of the sacral vertebræ are more or less reduced. In Anthropoids, and still more markedly in Man, the first sacral vertebra is plainly marked off from the last lumbar by the formation of the so-called *promontory*. A sacrum is wanting in the Cetacea and Sirenia, in correspondence with the absence of hind-limbs: the horizontal tail-fin in these forms is not supported by hard parts.

The caudal vertebræ vary extremely in their development, and excepting in most long-tailed Mammals—such as Kangaroos, Sirenians, Cetaceans, and certain Apes—no longer develop lower arches. When present these "chevron bones" are intervertebral in position.[2] The greatest number of caudal vertebræ is found in

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[1] A nodule of bone in the atlanto-occipital ligament of the Hedgehog may represent the vestige of a "pro-atlas" (p. 57).

[2] The question as to homology of the chevron bones, as well as of certain bony elements present in some Mammals beneath the intervertebral discs in the tail (*e.g.* Dasypus, Erinaceus) and lumbar region (*e.g.* Talpa), requires further investigation: it is doubtful to what extent they represent the lower arches or the intercentra of other Vertebrates, or are structures peculiar to Mammals.

Manis macrura (about fifty), and the caudal region is most reduced in the higher Primates, in which it forms a stump-like *coccyx* consisting of at most five to six vestigial vertebræ, all fused together, and these may even (*e.g.* in Man) unite with the sacrum.

In the human embryo of 4–6 mm. in length, a distinct tail is present, consisting of all the characteristic parts; it gradually undergoes reduction, and what is left no longer projects externally.

II. RIBS.

Some doubt still exists as to whether the ribs are to be considered as primitively independent skeletal structures, arising in the intermuscular septa or myocommas, or as parts of certain processes of the vertebræ which have become segmented off from the latter, as is plainly seen to be the case, for example, in embryos of Hatteria. Their relations to the axial skeleton, whether primary or secondary, are of the very closest kind.

The ribs are situated in the septa between the great lateral muscles of the body, and present much variation in the various vertebrate Classes: they may be short and stump-like and almost horizontal in position, or may grow ventralwards as delicate rod-like structures, so as to encircle the body-cavity more or less completely. Primitively, ribs may be present all along the vertebral column, but, especially in the higher types, they become reduced in certain regions.

A careful study of the ribs, in which their relations to the soft parts (muscles) is taken into consideration, shows that they are not completely homologous throughout the vertebrate series, and that those of most Fishes are not exactly morphologically comparable to those of Elasmobranchii, Amphibia, and Amniota.

Fishes.—Two kinds of ribs, situated at different levels, may be distinguished amongst Fishes—*dorsal ribs* and *ventral ribs* (or *pleural arches*): the former extend into the transverse septa which separate the epaxial or dorso-lateral from the hypaxial or ventro-lateral muscles, while the latter are situated internally to the muscles, just outside the peritoneum, but never more than partially encircle the cœlome (Fig. 50). Both kinds of ribs are usually considered as corresponding to prolongations of the transverse processses (basal stumps) of the vertebral axis, from which they have become segmented off but with which they remain closely connected: another view as to their primary origin has been stated above. The ventral ribs appear to be phylogenetically older structures than the dorsal ribs, which can only have originated after the differentiation of the intermuscular septa in which they are situated.

Towards the caudal region, the ventral ribs, together with the corresponding transverse processes, gr [illegible] take on the form of

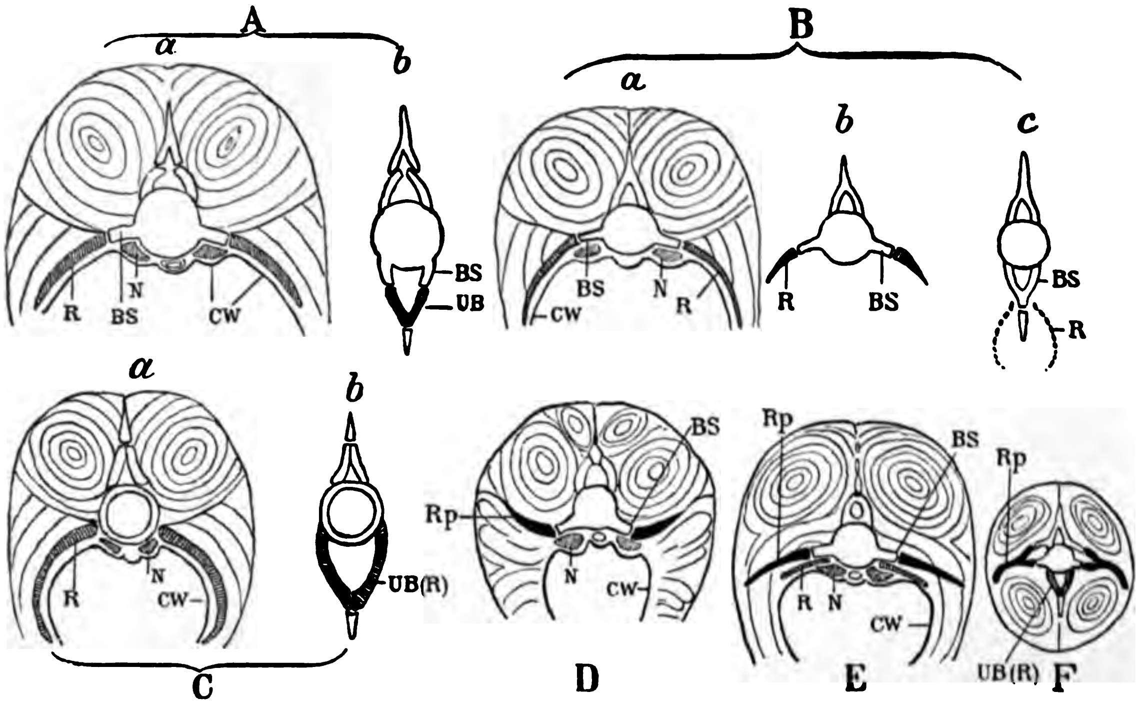

Fig. 50.—Diagrammatic Transverse Section of Various Vertebrates, showing the relations of the ribs and hæmal arches. Homologous parts are similarly shaded. A—Most Ganoidei, B—Teleostei, C—Dipnoi, D—Elasmobranchii, E—Polypterus, F—Amphibia (Urodela), through the base of the tail.

BS, transverse processes ("basal stumps"); *CW*, wall of cœlome; *N*, kidneys; *R*, ventral ribs, characteristic of most Fishes, which also appear in the form of hæmal arches (*UB*) in the caudal region of Dipnoans (*C*, *b*) and Urodeles (F); *Rp*, dorsal ribs, characteristic of Elasmobranchii, Amphibia, and Amniota; *UB*, hæmal arches. The figures also show the epaxial and the hypaxial muscles.

hæmal arches, which in Teleosts, as in Elasmobranchs, are developed from the transverse processes alone (Fig. 50, B). The dorsal ribs take no part in the formation of the hæmal arches: towards the posterior part of the trunk they become rudimentary, but may sometimes still be recognised in the tail as lateral processes at the bases of the hæmal arches.

In most *Ganoids* and in *Dipnoans* (Fig. 50, A, C) ventral ribs only are present. In *Crossopterygians* (Polypterus, Figs. 50, E, and 51) larger dorsal and smaller ventral ribs occur, so that there are two pairs of ribs to each body-segment. Dorsal ribs can also be recognised in certain *Teleosts* (Salmonidæ, Clupeoidei) in addition to ventral ribs, and like these, are always preformed in cartilage.[1]

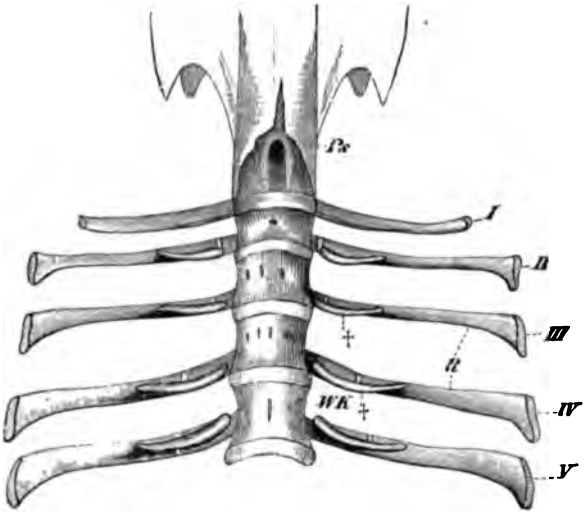

FIG. 51.—ANTERIOR END OF THE VERTEBRAL COLUMN OF POLYPTERUS. From the ventral side.

Ps, parasphenoid; *WK*, centra; *I—V*, first five pairs of dorsal ribs; ††, ventral ribs.

In many forms, the ventral ribs may undergo reduction, and in *Elasmobranchs* they are wanting, while dorsal ribs are usually present.[2] In Chimæroids and many Rays, as is also the case in Cyclostomes, a fibrous band extends outwards from the vertebral axis in the position usually occupied by dorsal ribs: thus these forms are ribless, and also in certain Teleosts and Ganoids the ribs are wanting (*e.g.* Lophobranchii) or quite vestigial (Polyodon).

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[1] This fact alone is sufficient to distinguish them from the *intermuscular bones* often present in this region in Teleosts. In addition to these *epicentral* intermuscular bones, others—the *epineurals* and *epipleurals*—are situated more dorsally and more ventrally respectively, and all of them are merely ossifications in the septa.

[2] The hæmal arches of these Fishes, as well as of Ganoids, Dipnoans, and Amphibians, apparently contain components corresponding to ventrals rib.

Amphibians.—The ribs in the Amphibia correspond to the dorsal ribs of Fishes, and are always connected with transverse processes or at any rate with the vestiges of the basal stumps (Fig. 50, F). The latter are originally situated, as in Fishes, towards the ventral side of the vertebral axis, and in the tail give

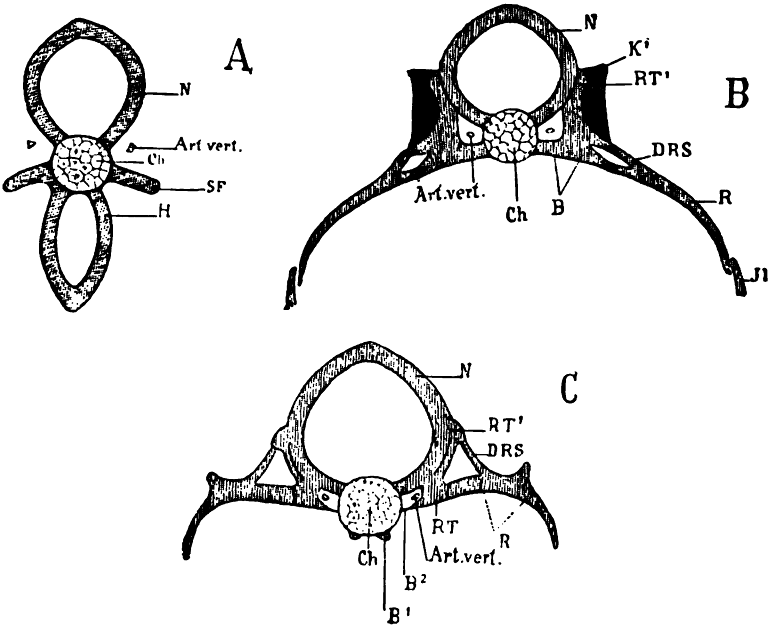

FIG. 52.—A, VERTEBRA FROM ANTERIOR PART OF TAIL OF LARVA (43 MM.) OF *Necturus*; B, SACRAL VERTEBRA FROM LARVA (43 MM.) OF *Necturus*; C, FOURTH TRUNK-VERTEBRA FROM NEWLY-BORN LARVA OF *Salamandra maculosa*. (After Göppert.)

Art. vert., vertebral artery; *B*, cartilage of basal stump; *B*¹, vestige of same in larva of Salamander; *B*², bony bar which replaces the same functionally; *Ch*, notochord; *DRS*, dorsal bar of rib; *Jl*, ilium; *N*, neural arch; *R*, rib; *RT*, *RT*¹, ventral and dorsal rib-bearing portions of vertebra; *SF*, lateral process of hæmal arch (*H*).

rise to hæmal arches (Necturus, Salamander-larvæ). In connection, apparently, with the more dorsal position of the horizontal inter-muscular septum in which they are situated, the transverse processes, even in Salamanders, tend to arise more from the neural arches than from the centra, and this upward displacement is carried still further in the Gymnophiona and Anura. In Urodeles (Fig. 52) the cartilaginous, rib-bearing basal stump is in close connection with the centrum, but gives off secondarily an upwardly directed process which becomes connected with the neural arch and on further development may serve as the chief point of attachment for the rib. The proximal part of the primitive basal stump is correspondingly reduced, and, with rare exceptions, is no longer developed: in its place is formed a bony bar, arising from the centrum, and generally not preformed in cartilage.

The ribs of the Urodela and Gymnophiona are bifurcated at their proximal ends, the ventral bar corresponding to the primary rib-rudiment, while the dorsal bar is a secondary structure formed in order to give the rib a firmer connection with the vertebra: in Urodeles it becomes connected with the rib-bearing portion of the vertebra, and in the Gymnophiona with the neural arch itself.[1]

The ribs of Amphibians are never very highly developed: they are only slightly curved and do not encircle the body-cavity to any extent. In Anurans they are not bifurcated and are very short and stump-like (Fig. 45), usually becoming fused with the transverse processes: they have doubtless undergone reduction.

In many Urodeles the ribs are limited to the trunk, but occasionally one or more pairs occur in the anterior part of the tail, where the basal stumps have already extended ventralwards to form the hæmal arches.

Finally, reference must be made to the cartilaginous "abdominal ribs" (cf. p. 42) developed in the ventral intermuscular septa in many Amphibians (Necturus, Menopoma, Bombinator).

Reptiles.—As already mentioned, the ribs of the Amniota are comparable to those of the Amphibia, but they grow further ventralwards and so encircle the body-cavity to a greater or less extent. Ribs may also be present in the tail: in Hatteria, for instance, there are seven or more pairs of caudal ribs.

The dorsal (proximal) section of the rib may also become segmented from the distal (ventral) portion,[2] and the former is plainly homologous with the Urodele-rib. As a rule a certain number of the ribs unite together ventrally to form a *sternum* (cf. p. 72 and Fig. 56): these are usually distinguished as "true" ribs from the others, or "false" ribs.

The ribs of Snakes show the least amount of differentiation; for, without giving rise to a sternum, they extend along the whole trunk from the third vertebra to the anal region, having a similar form and size throughout. In Lizards, in which a dorsal, unforked, bony portion and a ventral, cartilaginous portion can be distinguished, three or four ribs reach the sternum, and are not always completely segmented off from it. The proximal ends of the ribs of Hatteria are broadened out and articulate both with the centra and arches, thus indicating a differentiation into a capitulum and a tuberculum (cf. p 69.).

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[1] According to another view, the bifurcated amphibian rib is originally a double structure, the dorsal bar of the fork originating independently and only uniting secondarily with the ventral bar.

[2] An intermediate section also occurs in Crocodiles and many Lizards.

In Chelonians the cervical ribs unite with the vertebræ more or less completely, and in the region of the trunk the ribs become broadened out to form the costal plates of the carapace (p. 43).

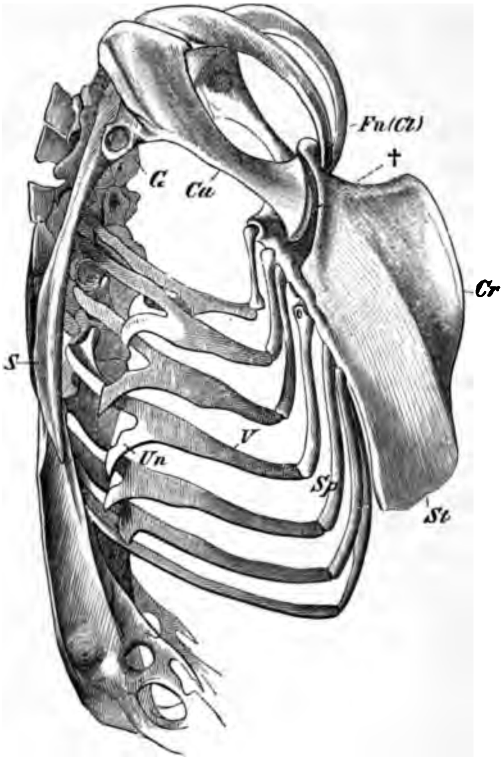

FIG. 53.—SKELETON OF THE TRUNK OF A FALCON.

Ca, coracoid, which articulates with the sternum (*St*) at † ; *Cr*, keel of sternum ; *Fu*(*Cl*), furcula (clavicles) ; *G*, glenoid cavity for humerus ; *S*, scapula ; *V*, vertebral, and *Sp*, sternal, portion of rib ; *Un*, uncinate process.

Their proximal unbifurcated ends are attached between the centra, at the junction of centrum and arch. There is no sternum.

The proximal ends of the cervical ribs in the Crocodilia are bifurcated, in correspondence with the double transverse processes in this region, and thus a vertebrarterial canal is formed (cf. p. 59). Further back, the ribs increase in length, and become segmented into two or three articulated portions. In passing from before backwards, their point of origin becomes gradually shifted, so that while the anterior thoracic ribs are attached to the centra, the posterior ones arise entirely from the transverse processes, which increase in size correspondingly. Eight or nine ribs reach the sternum, and from the eighteenth vertebra backwards the transverse processes no longer bear ribs, but only short cartilaginous apophyses.

Flat, curved cartilages, or *uncinates*, are present in connection with the ribs in the Crocodilia as well as in Hatteria.

Birds.—The ribs of Birds exhibit a much more marked segmentation into vertebral and sternal portions, both of which become ossified, and this evidently stands in relation to their more active respiration. Bony *uncinates*, comparable to those mentioned above, arise from, and usually become ankylosed to, the vertebral portions in nearly all Birds, and overlap the ribs next behind them (Fig. 53). The whole costal apparatus is usually rendered still firmer by the fusion of many of the trunk vertebræ (p. 60), by the individual ribs often being very broad, as well as by the form and arrangement of the sternum and pectoral arch. The last three or four cervical vertebræ may bear comparatively large and movable ribs. The number of ribs which articulate with the sternum varies between two (Dinornis elephantopus) and nine (Cygnus). The delicate ribs of Archæopteryx (Fig. 49) more nearly resembled those of Lizards.

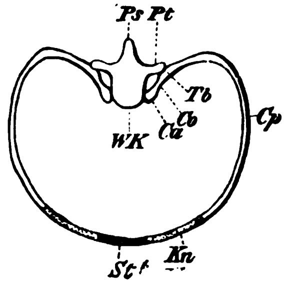

FIG. 54.—COSTAL ARCH OF MAN.

Ca, capitulum; *Co*, neck, *Cp*, bony vertebral, and *Kn*, cartilaginous sternal portion of rib; *Ps*, neural spine; *Pt*, transverse process; *St*, sternum; *Tb*, tuberculum; *WK*, centrum of vertebra.

Mammals.—The cervical ribs in nearly all cases unite completely with the vertebræ, and a vertebrarterial canal is thus formed. The last cervical rib may be well developed and may articulate with the corresponding vertebra (*e.g.* Cholœpus hofmanni).[1] The seventh cervical rib is also long in Bradypus, and the eighth and ninth ribs do not reach the sternum; they may therefore be counted as cervical. There is considerable variation with regard to the number of ribs which reach the sternum (*e.g.* in Manatus 2–3, in Cebus and Ateles 10): and in some cases the sternal, as well as the vertebral ribs may become ossified. In the vertebral portion a *capitulum*, a *neck*, and a *tuberculum* may be distinguished (Fig. 54). The capitulum usually articulates with its own centrum as well as with that next in front, in the region of the epiphysis; the tuberculum articulates with the cartilaginous facet on the transverse process. In the "false" ribs, these characters become to a greater or less extent lost in passing from before backwards, so that the posterior ribs have a more rudimentary character. As already mentioned (p. 62), vestiges of ribs are present in the lumbar and sacral regions, and unite with the corresponding transverse processes. There are usually thirteen pairs of ribs, but their number may vary between nine (Hyperoodon) and twenty-four (Cholœpus). These facts indicate that there has been a gradual phylogenetic reduction in the number of ribs, and the occasional presence of supernumerary ribs is to be explained as a reversion.[1]

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[1] As amongst Reptiles, the ventral cartilaginous portions of some of the anterior "false ribs" are connected with those in front, while the posterior ribs end freely in the body-wall ("costæ fluctuantes").

III. STERNUM.

Never present in Fishes, the sternum appears for the first time in **Amphibians** in the form of a small variously-shaped plate of cartilage situated in the middle line of the chest (Fig. 55). It arises as a paired cartilaginous plate[2] derived in the first instance from chondrifications in an intermuscular septum on the median border (linea alba) of the rectus abdominis muscle, and therefore may be looked upon as comparable to a pair of "abdominal ribs." Such cartilaginous structures must have been present in greater numbers in the ancestors of existing Urodeles (cf. p. 67). In many tailless Batrachians (*e.g.*, Ranidæ) the ventral portion of the pectoral arch is continued forwards in the middle line, from where the two clavicles meet, as a slender rod, the *omosternum* (Fig. 55, D): this has a similar origin, and the proximal portion both of it and of the sternum becomes ossified. Thus the sternum and omosternum of Amphibians are not to be considered as corresponding to differentiations of the pectoral arch (coraco-sternum), a view which is often held, but as consisting of skeletal parts which primarily belong to the body-wall, and only secondarily come into connection with the limb-skeleton.

In most Urodeles and certain Anurans (*e.g.* Pipa, Discoglossus, Bombinator, Alytes), this cartilaginous sternal plate is inserted into the grooved median margins of the two overlapping coracoids (Fig. 55, B, C). In Rana, on the other hand (D), in which the two

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[1] A primitive and a secondary type of thorax may be distinguished. The former is the more usual, and occurs in most Mammals even up to the lower Apes: it is characterised by an elongated form, and by the dorso-ventral diameter being much greater than the transverse diameter. The latter occurs in anthropoid Apes and Man, in which the dorso-ventral diameter has, both ontogenetically and phylogenetically, become considerably reduced relatively: the broad thorax is thus more cask-like in form, and may often even be flattened dorso-ventrally. A somewhat similar modification is seen amongst insectivorous Bats.

[2] It is unpaired from the first in Triton and Rana, but this is probably due to an abbreviation of development.

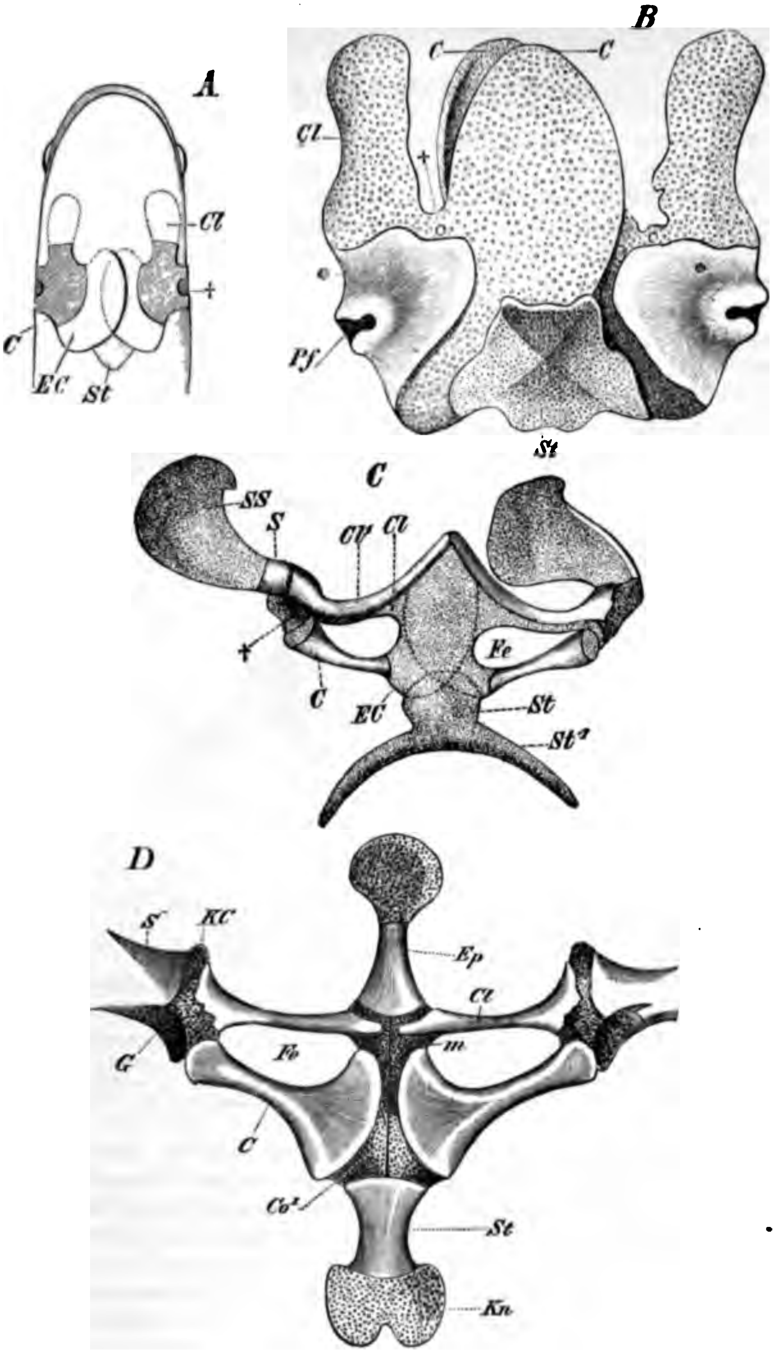

FIG. 55.—PECTORAL ARCH OF VARIOUS AMPHIBIANS. From the ventral side. A—Urodele (diagrammatic); B—Axolotl (*Amblystoma*); C—*Bombinator igneus*; D, *Rana esculenta*.

C, coracoid; *Cl*, procoracoid; Cl^1 (*Cl* in D), clavicle; *EC*, Co^1, epicoracoid; *Ep*, omosternum; *Fe*, fenestra between procoracoid and coracoid bars; *Kn*, cartilaginous xiphisternum; †, *Pf*, *G*, glenoid cavity for the humerus; *S*, *scapula*; *SS*, *suprascapula*; *St*, St^1, sternum. *, † (in B) indicate nerve-apertures.

halves of the pectoral arch are much more closely connected in the middle line, by far the greater part of the sternum lies entirely posterior to the coracoids, which do not overlap one another. In the Perennibranchiata and Derotremata the sternum is much simpler than in other Amphibians, and in Proteus and Amphiuma it is entirely wanting.

In the **Amniota,** the form of the sternum, like that of the pectoral arch, depends largely on the nature and function of the forelimbs. It is usually considered as arising primarily by a number of ribs running together ventrally so as to form a continuous cartilaginous longitudinal tract on either side. By the more or less complete fusion of these two tracts, an unpaired sternal band or plate is formed, from which the ribs are secondarily segmented off by the formation of articulations, and beneath which a dermal episternum is present in some cases (p. 44). The main part of the anterior end of the sternum of Mammals is formed by the median union of the first two or three pairs of cervical ribs, and beneath and in front of this region in Monotremes is a large T-shaped bone, the *prosternum* ("episternum"), the lateral parts of which come into relation with the clavicles (Fig. 103).[1]

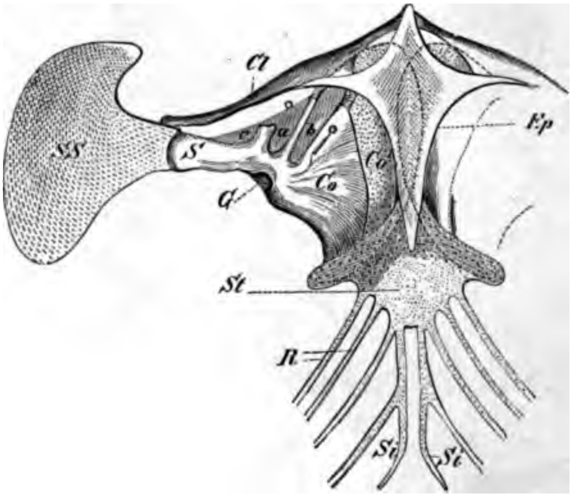

FIG. 56.—PECTORAL ARCH AND STERNUM OF A GECKO (*Hemidactylus verrucosus*). From the ventral side.

a, *b*, *c*, membranous fenestræ in the coracoid; *Co*, coracoid; *Co*¹, cartilaginous epicoracoid; *Cl*, clavicle; *Ep*, episternum; *G*, glenoid cavity for the humerus; *R*, ribs; *S*, scapula; *Si*, cartilaginous cornua to which the last pair of ribs is attached; *SS*, suprascapula; *St*, sternum.

The sternum may become calcified (Reptiles), or converted into true bone (Birds, Mammals). In Reptiles,[2] Birds, and Monotremes, the coracoids, as in Amphibians, come into direct connection with the lateral edges of the sternum (Figs. 53, 56, and 103), and in other Mammals, the clavicles, when present, are connected with it directly or indirectly.

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[1] Cf. note on p. 44.

[2] In Snakes and Chelonians there is no trace of a sternum.

The sternum is greatly developed in Birds, and consists of a broad, more or less fenestrated plate, provided in the vast majority of Carinatæ with a projecting keel, which forms an additional surface for the origin of the wing-muscles (Fig. 53). In contrast to these, the cursorial Ratitæ are characterised by a broad, more or less arched, shield-like sternum without a keel. In some flightless Carinatæ, however, the keel is rudimentary or even absent, and the vestige of a keel may occur, though not constantly, in certain Ratitæ. The presence or absence of a keel is not, therefore, a constant character separating these two groups of Birds from one another.[1]

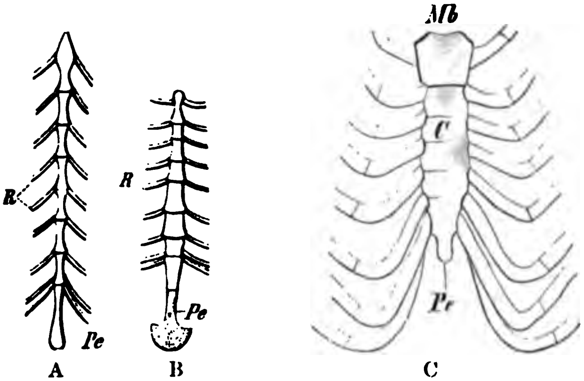

FIG. 57.—A, STERNUM OF FOX; B, OF WALRUS; AND C, OF MAN. From the ventral side.

C, body; *Mb*, manubrium; *Pe*, xiphoid process; *R*, ribs.

A far greater number of ribs are as a rule concerned in the formation of the sternum of Mammals than is the case in Reptiles and Birds. Consisting at first of a simple cartilaginous plate, it later becomes segmented into definite bony portions (*sternebræ*) the number of which may correspond to the affixed ribs (Fig. 57, A, B): in other cases as, for instance, amongst Primates (C), the individual bony segments may run together to form a long plate (*corpus sterni*). Its proximal end forms a more or less distinct *manubrium*, and the distal end a partly cartilaginous *xiphoid* or *ensiform process*.

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[1] A keel was also present in the Pterosauria, and may be developed wherever a larger surface for the origin of the pectoral muscles is required (*e.g.* Cheiroptera).

IV. SKULL.

General Part.

The question as to the primary origin of the skull in the Craniata has always taken a foremost place amongst the morphological problems relating to the structure of Vertebrates; and the first point which requires elucidation relates to the nature of the head—whether it is a structure *sui generis*, or whether its parts are due to modifications and further developments of parts present in the trunk.

Until past the middle of the present century the theory which held the field was the "vertebral theory" of Goethe and Oken, according to which the skull consisted of a number of modified vertebræ ("cranial vertebræ"). On this theory, therefore, the skull was regarded as a special modification of the anterior part of the vertebral column, and a large number of facts were brought forward in support of it: even when morphological science had made further considerable advances, there still seemed to be a certain amount of justification for this view.

The arguments in support of the vertebral theory of the skull may be briefly stated as follows. As in the vertebral column, a *cartilaginous* and a *bony stage* may be distinguished in the skull, ontogenetically as well as phylogenetically. There is thus an important correspondence between these two parts of the craniospinal axis, and this is further emphasised by the fact that the notochord always extends for a certain distance into the base of the skull, so that the latter is developed on the same skeletogenous basis as, and in direct continuation of, the vertebral axis. Moreover, the cranial cavity, enclosing the brain, may evidently be considered as a continuation of the neural canal.

For a long time it was not recognised that as this theory depended on giving an exact account merely of the skeletogenous elements taking part in the formation of the skull, it could not possibly lead to a true interpretation of the origin of the vertebrate head. Any such attempt meant "putting the cart before the horse," by looking upon the last acquisition of the head —its skeleton—as the leading point for future researches.

Although it gradually became evident that, except occasionally in the hinder (occipital) region, no trace of segmentation of the cartilaginous elements can be recognised in the head of any existing Craniata, it still seemed to be an open question whether such a segmentation may not have occurred in early phylogenetic stages and have gradually become suppressed owing to deep-seated physiological and morphological modifications.[1]

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[1] It is still by no means clear whether or not the sense-capsules were primitively independent of the rest of the axial part of the skull, and it is quite conceivable that the part of the latter anterior to the vagus foramen consisted originally of independent skeletal portions which only secondarily became connected with one another.

The *original* segmentation of the head—*i.e.*, the segmentation of the mesoderm into somites—may have more or less closely resembled that seen in Amphioxus; but it must be borne in mind that there is no direct connection between the Acrania and Craniata, and that there must have been a whole series of intermediate forms. As a matter of fact, only vestiges of the primary metamerism of the head have persisted, and are more or less plainly indicated ontogenetically by the ganglia, nerves, gill-arches, and myomeres. It is nevertheless certain that the structural plan of the head, like that of the trunk, is based on a condition of metamerism, although it is doubtful how many primary segments are included, and whether segmentation is not limited to the post-auditory region (chordal or "spinal" portion) of the skull, and does not concern the more anterior (prechordal or "prespinal") portion.

In any case, however, the metameric character is much more plainly seen in the post-auditory (occipital) region than in the more anterior part of the head, in which the primary relations are no longer recognisable owing to parts having become reduced, displaced, fused, lost, or functionally changed in connection with the modifications resulting from the development of the brain, skull, the olfactory, optic, and auditory organs, and the oral muscles. A reduction, fusion, or loss of cephalic myotomes has also occurred in the post-auditory parts, the occipital region being of a very varied and fluctuating nature, and it may even include spinal elements. It is therefore evidently impossible in this place to give more than the briefest sketch of the problem under consideration before making a detailed study of the parts composing the head.

The portion of the skull which is situated along the main axis in continuation of the vertebral column and which encloses the brain, is known as the *brain-case* or *cranium* (*neurocranium*), and is primarily composed of cartilage. A series of cartilaginous arches arise in serial order on the ventral side of the brain-case; these encircle the anterior part of the alimentary tract like hoops, incomplete dorsally, and are distinguished as the *visceral portion* of the skull (*splanchnocranium*). This bears an important relation to branchial respiration, as between each consecutive pair of arches a passage (gill-cleft) lined by endoderm, is present, communicating between the pharynx and the exterior, and through which the water passes in branchiate forms: the foremost visceral arch, which bounds the aperture of the mouth, becomes modified to form the skeleton of the *jaws*. The arches, therefore, serve primarily as gill-supports. Ossification may occur in connection with the cranial and visceral portions later.

Before the cartilaginous skeleton begins to be formed in the embryo, the greater part of the head consists of a mesodermic formative tissue, which gives rise to a membranous capsule around the brain and in which the rudiments of the individual cerebral nerves can be plainly distinguished. The paired olfactory, optic, and auditory *organs also* appear at a very early stage; and these, in the course of further development, become situated in bays or cavities within the head and enclosed by definite sense-capsules, which take on close relations with the cranium, and thus are of extreme importance in modifying the configuration of the skeletal structures which are formed around them later.

The relations of the visceral to the cranial skeleton, and those of both to the primary metamerism of the head, must be taken into consideration. Both cranial and visceral regions must have been originally segmented, and each myotome at one time included a ventral portion (lateral plate of the mesoderm) which enclosed a corresponding section of the cranial cœlome, or " head-cavity." Later, however, the visceral region became relatively shifted to a greater or less degree, especially in the anterior part of the head, so that its segments no longer corresponded to those of the cranial region, which is in general more conservative as regards its metamerism. Thus we find that the segmentation of the nervous, muscular, and visceral parts of the head do not correspond with one another.

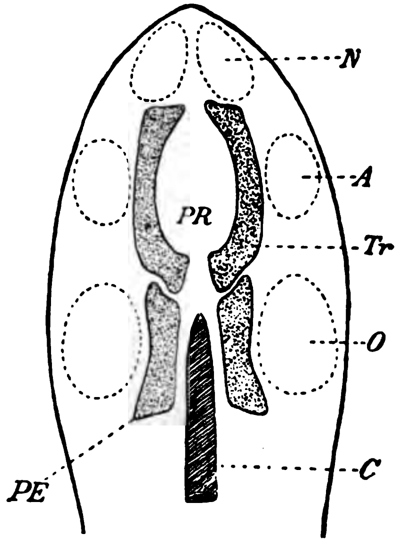

FIG. 58.—FIRST CARTILAGINOUS RUDIMENTS OF THE SKULL.

C, notochord; *N*, *A*, *O*, the three sense-capsules (olfactory, optic, and auditory); *PE*, parachordal elements; *PR*, primary pituitary space; *Tr*, trabeculæ cranii.

a. Brain Case (Neurocranium).

The first cartilaginous rudiments of the primordial skull or *chondrocranium* are seen in the form of an anterior and a posterior pair of bars—the *trabeculæ cranii* and the *parachordal* cartilages

(Figs. 58 and 59), which may be continuous with one another. They lie along the base of the brain, the parachordals embracing the anterior end of the notochord. The parachordals soon unite, more or less completely, to form a *basal plate*, which grows round the notochord dorsally and ventrally, and thus early forms a solid support for the hinder part of the brain. The trabeculæ project forwards and enclose a space, which, as the pituitary body extends from the brain through its posterior part, may be spoken of as the primitive *pituitary space* (*anterior basicranial fontanelle*). In the parachordal region, an anterior *auditory* or *otic*, and a posterior *occipital* portion, may be recognised on either side. The occipital region, as already mentioned, may show indications of segmentation in the nerve-apertures which perforate the cartilage as well as in the surrounding myomeres: its anterior limit is marked by the vagus nerve.

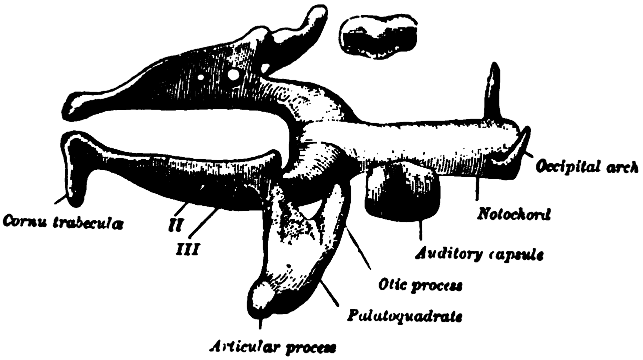

FIG. 59.—NEUROCRANIUM AND PALATOQUADRATE OF LARVAL AMBLYSTOMA, 9 MM. IN LENGTH, SEEN OBLIQUELY FROM THE LEFT SIDE AND ABOVE. × ABOUT 35. (From copy by Fr. Ziegler of a model by Ph. Stöhr.)

II, foramen for optic nerve, and III, for oculomotor nerve.

Around the auditory organ of either side is developed, usually independently, a cartilaginous *auditory capsule* (Figs. 59–61), which is relatively larger in the lower than in the higher Vertebrates. It is situated laterally to the otic region, between the trigeminal and vagus nerves, and becomes closely connected with the corresponding parachordal which may help to complete it.

The trabeculæ may remain separated from one another or may become united along the greater part of their length under the influence of the developing *optic capsules*. In the former case the skull may be described as *platybasic*, and the brain extends forward interorbitally to the ethmoidal region (many Elasmobranchii, Dipnoi, Amphibia, Fig. 60); in the latter, or *tropibasic* type (Fig. 61), the trabeculæ give rise to a thin interorbital septum, and the brain only extends as far forward as this septum, in the dorsal part of which a narrow canal encloses the olfactory lobes or nerves.

The further development of the wall of the orbital or orbito-temporal fossa takes place either from the trabeculæ or independently of them, and during its growth, the cartilage extends round a number of the cerebral nerves. The anterior ends of the trabeculæ, which are continuous with the *ethmoidal region* of the skull, vary much in form in different Vertebrates according to whether the skull is of the platybasic or tropibasic type. The ethmoidal skeleton may be completed in various ways by the cartilaginous *nasal* or *olfactory capsules*, the chondrification of which takes place independently in the connective tissue surrounding the nasal sacs. Anteriorly, the ethmoidal region may extend forwards to form a rostrum, or prenasal cartilages may be formed.

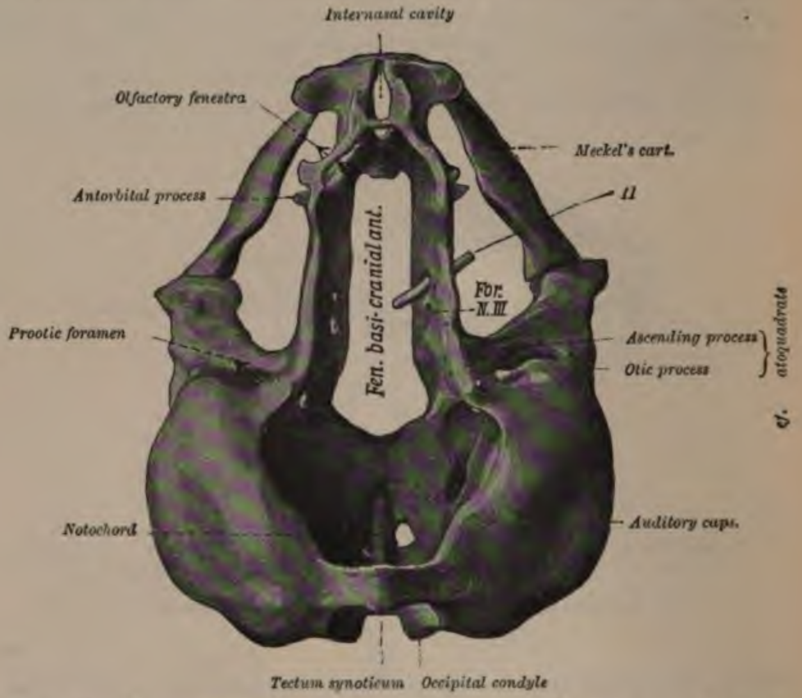

FIG. 60.—NEUROCRANIUM (PLATYBASIC TYPE) AND MANDIBULAR ARCH OF LARVAL NEWT (*Triton tæniatus*), 2 CM. IN LENGTH, SEEN FROM ABOVE. × 25. (From a model by E. Gaupp.)

The olfactory and auditory capsules, especially in higher types, then become more and more drawn in to the skull proper, and the lateral edges of the basal plate begin to grow upwards round the brain on both sides, eventually extending even to the dorsal region. Thus a continuous cartilaginous neurocranium is formed such as persists throughout life in Elasmobranchs, for example. But in by far the greater number of Vertebrates, the cartilage does not play so great a part, and is, as a rule, confined to the base and lower parts of the sides of the skull and to the sense capsules, except in the occipital region, where it always extends over the brain. The rest of the skull, more particularly the roof, becomes directly converted from membrane into bone (investing bones): at the same time, bones may become differentiated in connection with the chondrocranium itself, which is thus more or less completely replaced by an *osteocranium*. In general, the higher the systematic position of the animal, the less extensive are the cartilaginous constituents and the more important the bony elements.

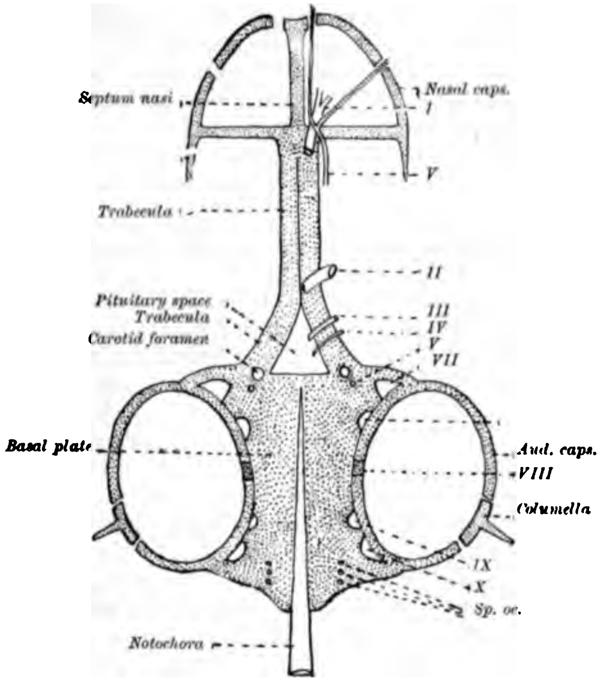

FIG. 61.—DIAGRAM OF A TROPIBASIC PRIMORDIAL SKULL, BASED ON THE CONDITIONS SEEN IN THE AMNIOTA, AND SHOWING THE RELATIONS OF THE MORE IMPORTANT FORAMINA. (After E. Gaupp.)

The cerebral nerves or their foramina are indicated by Roman numerals: *Sp. oc.*, foramina for spino-occipital nerves.

The *investing bones* (*allostoses*) have originally no direct connection with the chondrocranium, and thus may be contrasted with those bony elements which are formed in close relation with it, both phylogenetically and ontogenetically. These perichondral bones extend into the cartilage and many even entirely replace it ("endochondral" bones); they may therefore be called *replacing* or *substituting bones* (*autostoses*) (cf. p. 45). It must, however, be borne in mind that the stage of development at which the different bones appear gives no accurate basis for phylogenetic speculations: bones which correspond in position as well as in other respects and thus appear to be homologous, may be developed in different ways in different Vertebrates.

The development of bones starts from so-called "centres of ossification," of which there may be several in a single resulting bony territory. An earlier or later fusion of these centres or even of entire bones, leads to a reduction in number; while on the other hand, "supernumerary bones" may occur owing to the absence of fusion between separate centres.

b. The Visceral Skeleton (Splanchnocranium).

The primarily cartilaginous visceral arches, which are developed successively from before backwards in the lateral plates of the mesoderm, encircle the anterior section of the alimentary canal, and are situated in the interbranchial septa (Figs. 62 and 63). The branchial apparatus at first lies beneath the hind-brain, and the arches are thus included under the cranial skeleton, of which, however, they are mostly genetically independent. Later, owing to unequal growth, most of the gill-sacs become relatively shifted backwards so as to be situated in the region of the trunk. The visceral arches are always more numerous (in some cases there are as many as nine) in forms which possess gills than in higher types (Amniota), in which their number gradually becomes reduced from behind forwards: they may, moreover, undergo a change of function, certain of them in some cases taking on definite relations to the auditory organ, larynx, and tongue.

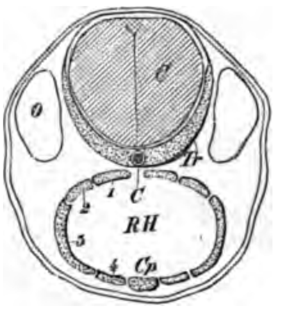

FIG. 62. — DIAGRAMMATIC TRANSVERSE SECTION OF THE PRIMORDIAL SKULL.

C, notochord; *O*, auditory capsule; *RH*, cavity of the pharynx, enclosed by the visceral skeleton; 1 to 4, the individual elements composing each visceral arch, which is united with its fellow by a basal piece (*Cp*); *Tr*, trabeculæ, which enclose the brain (*C*) ventrally and laterally.

The most anterior arch arises first and serves as a support for the walls of the mouth which receive their nerve supply from the trigeminal: it is distinguished from the other or *post-oral arches* as the *mandibular arch* (Fig. 63). The post-oral arches serve as gill-bearers in the Anamnia, but even the first of them, the *hyoid*, along which the facial nerve extends, becomes modified from those lying behind it: these, the *branchial arches* proper, of which there are usually five in Fishes, are in relation with the glossopharyngeal and vagus. All the visceral arches must originally, however, have borne gills.

Primarily unsegmented, the individual post-oral arches may become divided up into portions (*pharyngo-*, *epi-*, *cerato-*, and *hypohyal* or *branchial*), the uppermost of which lies under the base of the skull, while the lowermost is connected with its fellow by a median basal piece or *copula* (*basihyal, basibranchial*).

The mandibular arch also undergoes segmentation, and becomes divided into a short proximal piece, the *quadrate*, and a long distal *mandibular* or *Meckel's cartilage* (Fig. 63). The quadrate gives rise anteriorly to a process, the *palatoquadrate* or *palatopterygoid*, which usually becomes fixed in various way to the base of the skull and gives rise to the primary upper jaw, Meckel's cartilage forming the lower jaw.

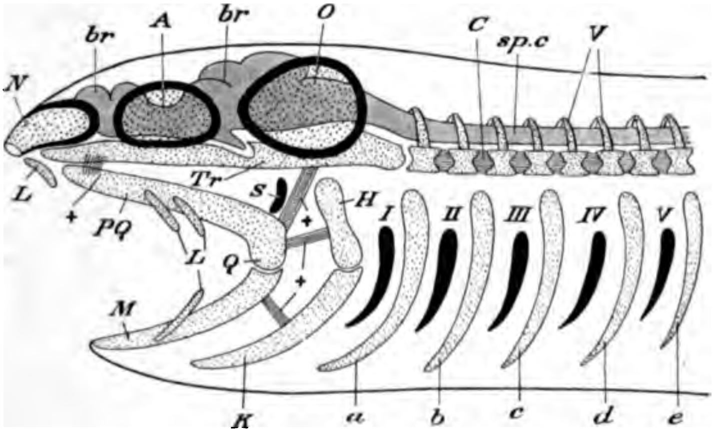

FIG. 63.—DIAGRAMMATIC FIGURE OF AN EMBRYONIC ELASMOBRANCH SKULL, SHOWING THE RELATIONS OF THE VISCERAL ARCHES.

A, eye; *a* to *e*, branchial arches, between which the gill clefts (*I* to *V*) are seen; *br*, brain; *C*, intervertebral remains of notochord; *H*, hyomandibular; *K*, hyoid arch; *L*, labial cartilages; *M*, Meckel's cartilage; *N*, nasal capsule; *O*, auditory capsule; *PQ*, *Q*, palatoquadrate, connected with the trabecula by ligaments at †; *S*, spiracle; *sp.c*, spinal cord; *Tr*, trabecula; *V*, vertebral arches.

The quadrate, which primarily serves as a support (*suspensorium*) for the jaws, either remains separated from the skull, being only connected with it by an articulation or by connective tissue, or becomes united with it.

The hyoid may also take part in the suspensorial apparatus, and thus come into close relation to the mandibular arch and cranium: its upper element (pharyngohyal), articulating with the skull to form the suspensorium, is then known as the *hyomandibular* (Fig. 63), and from it (*e.g.*, in Teleosts) a *symplectic* may be differentiated distally.[1] In the mid-ventral line there is a basihyal connecting the arch of either side and embedded in the tongue (*entoglossal* or *glossohyal*).

Certain smaller or larger skeletal parts of doubtful homology form a kind of outwork to the skull anteriorly, and have been described as *precranial* or *preoral elements.* Under this category are included the *labial cartilages* of Elasmobranchs (Fig. 63), and similar structures amongst Teleostomes and in certain Anuran larvæ.

Relations of the Chief Investing Bones to the Chondocranium.

The primary relations of the investing bones to definite parts of the cartilaginous skull are not in all cases sufficiently known, but the following scheme, formulated by Gaupp, probably holds good as regards the more important elements (cf. under Special Part and Figs. 67–95).

The *parietals* and *frontals* are primarily situated on the roof of the skull in the auditory and orbitotemporal regions, beyond which they may, however, extend. The *squamosal*, which in the Amniota is developed on the outer wall of the auditory capsule, is also present in Bony Ganoids and Teleosts, but in them loses the character of an investing bone (cf. p. 83).[2]

The investing bones of the ethmoidal region are: the *nasal*, *supraethmoid* of Teleostei, *prefrontal* of Amphibia and Sauropsida, *septomaxillary* (situated in the posterior region of the nasal fenestra in Amphibia and Reptilia, and sometimes extending into and beyond the nasal capsule), and the *lacrymal* of Mammalia; it is doubtful whether the last mentioned corresponds to the similarly-named bone of Lizards and Crocodiles. The relations of the *premaxilla*, *maxilla*, and *vomer* to the ethmoidal skeleton are possibly of a secondary nature (cf. p. 83). The *parasphenoid* arises in the mucous membrane beneath the cranial floor.

On the lateral surface of the palatoquadrate of Amphibians is an extensive bone, usually known as the squamosal, but called the *paraquadrate* by Gaupp, who considers it to be homologous with the *quadratojugal* of Reptiles. The *vomer*, *palatine*, and *pterygoid* (including the *ecto-* and *ento-pterygoids* of Teleosts) probably arose as tooth-bearing investing bones on the palatine region of the palatoquadrate, and are therefore traceable to the teeth which in Elasmobranchs are present along the cartilaginous upper jaw. In Teleosts, however, the vomers, and in Amphibians the palatines also, are no longer situated on parts of palatoquadrate, but are related to the ethmoidal skeleton, and lie beneath the olfactory capsules. The pterygoid alone retains its original relations to the palatine bar in Amphibians and many Reptiles.

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[1] It is possible that the hyoid arch is the derivative of two arches which were primarily separated by a cleft.

[2] The primary relations of the postfrontal and jugal of the Amniota cannot at present be stated.

The palatoquadrate cartilage, which in Elasmobranchs is situated along the upper margin of the mouth, represents the primary upper jaw, and does not correspond to the premaxillo-maxillary bar which lies externally to it in the higher Fishes and in all Vertebrates above them. It is possible that the premaxillæ and maxillæ were originally laid down in relation with certain of the labial cartilages referred to above (p. 82, Figs. 63, 65, and 66.)

In the lower jaw, investing and tooth-bearing bones are formed around Meckel's cartilage. As in the upper jaw, two bars, an outer and an inner, may be distinguished, the former represented by the *dentary* and the latter by the *splenial*, in connection with which there may be a varying number of *presplenials*. As the teeth on the primordial lower jaw of Elasmobranchs may be looked upon as corresponding to splenial teeth, it is possible that the dentary, like the premaxilla and maxilla, may have been originally formed around a primary skeletal element situated anteriorly to the primitive jaw.

The purely integumentary ossifications also of the lower jaw are investing bones of Meckel's cartilage: great confusion exists as regards their nomenclature ("*dermangular*," "*dermarticular*," "*supra-angular*," "*coronary*").

Certain tooth-bearing bones are formed in connection with the hyobranchial skeleton of Teleosts (*superior* and *inferior pharyngeal bones*, "*dermobranchials*," "*dermentoglossal*"). In higher forms, investing bones are only exceptionally present in connection with this part of the primordial skeleton.

Relations of the Replacing Bones.

The following are usually looked upon as ossifications of the occipital region (cf. Figs. 67–95): the *basioccipital*, *exoccipitals* (*pleuroccipitals*), and *supraoccipital*: the last mentioned, however, usually arises from the ossification of that part of the roof of the skull (*tectum synoticum*, Fig. 60) which belongs to the auditory region. The supraoccipitals and exoccipitals usually extend into the auditory capsules, in each of which (otic region) arise the ***periotic bones***, including an *opisthotic*, *epiotic*, *prootic*, *sphenotic*, and ***pterotic***: of these, the most constant element is the prootic. The sphenotic and pterotic occur only amongst Fishes, in which, however, the pterotic does not remain independent, but unites with a dermal bone to form the squamosal, which is thus made up of an ***autosquamosal*** and a *dermosquamosal*.

In the orbito-temporal region, a *basisphenoid*, a *presphenoid*, *alisphenoids*, and *orbitosphenoids* may occur. In the ethmoidal region *lateral ethmoids* and *pre-ethmoids* are present in bony Fishes and a single ethmoid in Mammals.[1]

The quadrate region of the palatoquadrate usually becomes ossified as a *quadrate* bone. In Bony Ganoids and Teleosts there is also a *metapterygoid*, and an *autopalatine* at the anterior end of the palatine bar which mostly fuses with a dermopalatine.

An *articular* is usually formed at the proximal end of Meckel's cartilage, and anteriorly and posteriorly to this zone of ossification an *autocoronary* and other bones may be developed (Teleosts). The anterior end of Meckel's cartilage usually becomes ossified as a *mentomandibular* (*mentomeckelian*) which may become fused with the dentary.

In the hyobranchial skeleton, the individual segments may be uniformly ossified (*e.g. stylohyal*, *glossohyal*, and the segments of the branchial arches); but frequently several ossifications may occur in a single segment.

SPECIAL PART.

In **Amphioxus** the vestigial brain is merely surrounded by a thin layer of connective tissue, and there is no proper cranial skeleton. The margin of the oral funnel and the cirri arising from it are supported by cartilage-like skeletal rods. The branchial skeleton consists of a series of elastic rods of a cuticular nature, which are connected together dorsally by arched portions and by transverse bars at different levels, but which remain separate ventrally. A comparison between these and the branchial skeleton of higher forms is rendered all the more impossible by the fact that no definite boundary between the head and trunk can be recognised.

Fishes (including **Cyclostomes**).

The skull of Fishes exhibits very great differences in the various groups, and in many cases reaches a high degree of complication. It is therefore only possible to give here the merest sketch of its characteristic structure in the different Orders.

In **Cyclostomes**, the skull is developed essentially in the manner already described. Later, however, it shows many special peculiarities (Fig. 64), probably in consequence of the suctorial (Petromyzon) or parasitic (Myxine) mode of life of these animals: the most important of these is the absence of jaws such as are present in all other Craniata; for this reason these forms are spoken of as *Cyclostomata* to distinguish them from the other craniate Vertebrates or *Gnathostomata*.

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[1] It is still uncertain as to how far the replacing bones of the cranium called by the same names in different Vertebrate groups are really homologous.

In addition to the peculiar histological differences in the structure of the cartilage, many other special characters of the skull are seen not only in the Class as a whole, but also in the two Orders, which must have become specialised very early along different lines, so that a comparison between them is rendered difficult. The low character of the skull is marked by the imperfect development of the cartilaginous brain-box, and thus most of the cerebral nerves on making their exit from the skull are but slightly or not at all surrounded by cartilage: moreover, the anterior region of the spinal axis, which in Gnathostomes becomes assimilated to the cranium, remains undifferentiated, so that an occipital region is wanting and the vagus makes its exit behind the skull ("*palæocranium*") and not through its walls.

The jaw-apparatus has doubtless become degenerated, and indications of its former presence may possibly be recognised. Thus certain similarities between the subocular arch (Fig. 64, *sb. oc. a.*) and the palatoquadrate of the Frog-tadpole were pointed out by Huxley; the posterior lateral cartilage (*p.lat.c*) is perhaps comparable with Meckel's cartilage and the styloid process (*st.p*) and cornual cartilage (*cn.c*) with the hyoid. A number of other cartilages supporting the anterior parts of the head cannot well be directly compared with parts of the gnathostomatous skull.

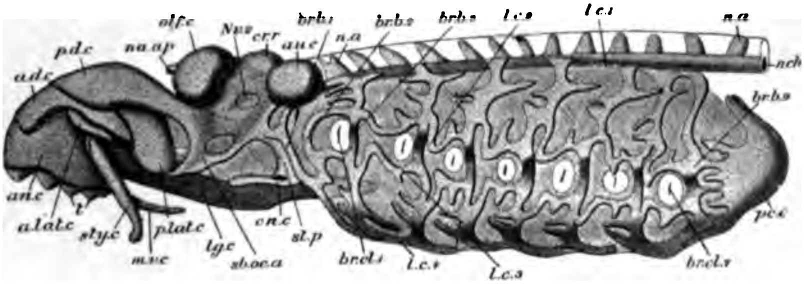

FIG. 64.—SKULL WITH BRANCHIAL BASKET OF *Petromyzon marinus*. (After W. K. Parker.)

The cartilaginous parts are dotted. *a.d.c*, anterior dorsal cartilage; *a.lat.c*, anterior lateral cartilage; *an.c*, annular cartilage; *au.c*, auditory capsule; *br.b*, *1—7*, vertical bars of branchial basket; *br.cl*, *1—7*, external branchial clefts; *cn.c*, cornual cartilage; *cr.r*, cranial roof; *l.c*, *1—4*, longitudinal bars of branchial basket; *lg.c*, lingual cartilage; *mv.c*, median ventral cartilage; *na.ap*, nasal aperture; *nch*, notochord; *Nv. 2*, foramen for optic nerve; *olf.c*, olfactory capsule; *pc.c*, pericardial cartilage; *pdc*, posterior dorsal cartilage; *p.lat.c*, posterior lateral cartilage; *sb.oc.a*, subocular arch; *st.p*, styloid process; *sty.c*, styliform cartilage; *t*, teeth.

In the adult Lamprey, for instance, the suctorial mouth is supported by various skeletal elements, amongst which may be mentioned a ring-like cartilage (*an.c*) around the margin of the dome-shaped oral funnel, between the dorsal side of which and the brain-case are a couple of large overlapping cartilages (*a.d.c, p.d.c*): the tongue is supported by a long, lingual cartilage (*lg.c*), and besides the other elements shown in Fig. 64, cartilages are present in the velum at the base of the oral funnel. On the mucous membrane covering the annular and lingual cartilages inside the oral funnel are a number of *horny teeth*. The fibro-cartilaginous olfactory sac is *unpaired*, and opens on the dorsal surface of the head by a single nostril. The visceral skeleton also shows many exceptional peculiarities: it consists of a series of unsegmented rods produced into short processes and

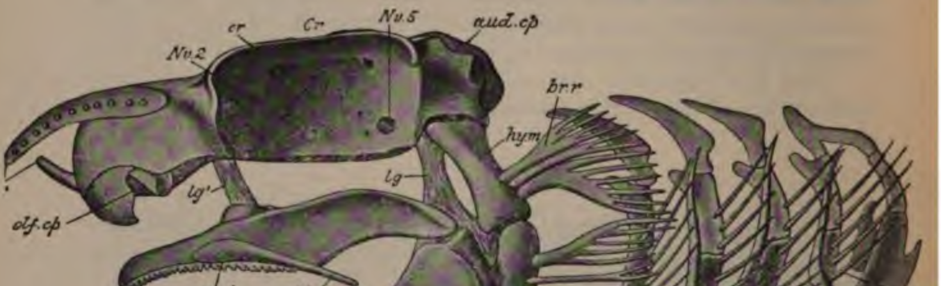

FIG. 65.—SKULL OF DOGFISH (*Scyllium canicula*). (From T. J. Parker's *Biology*, after W. K. Parker.)

aud.cp, auditory capsule; *br.a, 1—5* branchial arches; *br.r, br.r'*, branchial rays arising from the hyoid and branchial arches; *Cr*, cranium; *ex.br*, extra-branchial cartilages; *hy.cn*, ventral part of hyoid arch; *hy.m*, hyomandibular; *lb*, labial cartilage; *lg.lg'*, ligaments supporting the jaws from the cranium; *l.j*, Meckel's cartilage; *Nv. 2*, optic foramen; *Nv. 5*, foramen for trigeminal and facial nerves; *olf.cp*, olfactory capsule; *or*, orbit; *r*, rostral cartilage; *up.j*, palatoquadrate. (The spiracular cartilage is not indicated.)

connected with one another by longitudinal bars, the whole forming a delicate cartilaginous basket-work: the last bar is connected with a cartilage in the walls of the pericardium. This basket-work has a very superficial position.

In Myxine the branchial skeleton is rudimentary, and amongst other peculiarities, the long nasal passage is surrounded by cartilaginous rings and communicates with the pharynx by a naso-palatine duct.

No fossil Cyclostomes are known, but *Palæospondylus gunni* from the Old Red Sandstone of Caithness possibly shows affinities with this group.

In **Elasmobranchs** the skull presents the simplest conditions and most easily comprehensible relations, so that it may be taken as the starting-point for the study of the skull of all other Vertebrates. It consists of a simple cartilaginous and fibrous capsule more or less movably articulated with the vertebral column, the chondrocranium here reaching its highest development (Figs. 65 and 66), while from the Elasmobranchs onwards it undergoes, on the whole, a gradual reduction owing to the increasing importance of the osteocranium. The skull may become more or less calcified, but true bones are never formed. The fibrous portions (*fontanelles*) are most marked in the prefrontal region, except in the tropibasic skull of the Holocephali, in which there is no prefrontal fontanelle and the interorbital region consists of a thin membranous septum between the large eyes (Fig. 66).

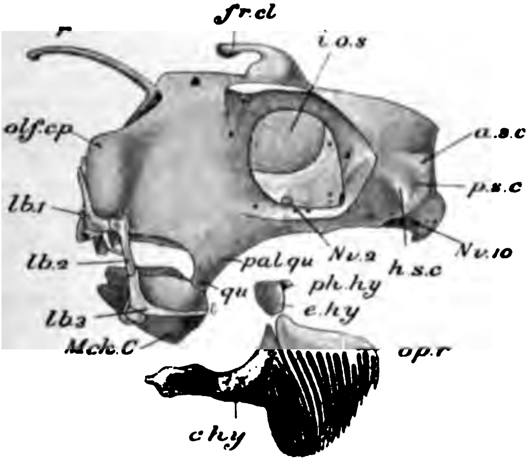

FIG. 66.—SKULL OF *Chimæra monstrosa*, LATERAL VIEW. (From Parker and Haswell's *Zoology*, after Hubrecht.)

a.s.c, position of anterior semicircular canal; *ch.y*, ceratohyal; *ep.hy*, epihyal; *fr.cl*, frontal clasper; *h.s.c*, position of horizontal semicircular canal; *i.o.s*, interorbital septum; *lb. 1*, *lb. 2*, *lb. 3*, labial cartilages; *Mck.C*, mandible; *Nv. 2*, optic foramen; *Nv. 10*, vagus foramen; *olf.cp*, olfactory capsule; *op.r*, opercular rays; *pal.qu*, palatoquadrate; *ph.hy*, pharyngohyal; *p.s.c*, position of posterior semicircular canal; *qu*, quadrate region; *r*, rostrum.

As in all Vertebrates above Cyclostomes, an assimilation of vertebral elements has taken in the occipital region, so that the nerves belonging to the vagus-group perforate the skull; the part of the skull situated posteriorly to these foramina has therefore been described as a "*neocranium*" (cf. p. 85).

The nasal region is often elongated to form a cut-water or *rostrum*, at the proximal end of which the olfactory sacs are situated, their cavities being separated from the cranial cavity by a membrane. Behind them are the deep orbital hollows, which are bounded posteriorly by the strongly projecting auditory capsules. *Labial cartilages* (cf. p. 82) are present in connection with the lips, nostrils, and jaws.

The palatoquadrate meets with its fellow in the middle line and is usually connected with the basis cranii by ligaments (Fig. 65). A process may be present on it which articulates at some point with the trabecular region. In the Chimæroids (Fig. 66) it becomes immovably fused with the cranium, whence their name of Holocephali. In the Sharks and Rays the palatoquadrate is not directly united to the skull, but is suspended from it by the hyomandibular (p. 82, and Fig. 65). In this case the skull may be described as *hyostylic*, to distinguish it from *autostylic* skulls, in which the hyoid takes no part in the suspensorium. In Notidanus, both mandibular and hyoid arches are independently connected with the skull, which is therefore spoken of as *amphistylic*. A vestigial cleft, the *spiracle*, is situated in front of the hyomandibular, and leads into the pharynx; on its anterior wall may be found remnants of the embryonic spiracular gill, beneath which are one or more *spiracular cartilages* which probably represent gill-rays (cf. below).[1]

In Plagiostomes the palatoquadrate and lower jaw are provided with numerous teeth, arranged in rows; in the Holocephali the teeth have the form of strong and sharp-edged plates.

The branchial skeleton is relatively smaller in the Holocephali than in other Elasmobranchs, in which it is always richly developed, and owing to secondary segmentation and also to fusion of its parts, exhibits characteristic modifications. On the outer circumference of each branchial arch, as well as on the hyomandibular and hyoid, radially-arranged cartilaginous rays are developed, which serve as supports for the gill-sacs (Fig. 65). Externally to these rays rod-like "extra-branchial" cartilages are present: these correspond to the displaced uppermost and lowermost gill-rays.

In Plagiostomes the gill-slits open freely on to the surface of the body, but in the Holocephali a fold of skin, the *gill-cover* or *operculum* arising from the hinder border of the hyomandibular, overlies them. In the frilled Shark (Chlamydoselachus) there is an indication of an operculum.

Amongst **Ganoids,** the lowest condition is met with in those forms in which the hyaline primordial skull is still retained, immovably fixed to the vertebral axis, part of which becomes secondarily assimilated to it. These forms are spoken of as Cartilaginous Ganoids. The presence of definite bones, however, divides them sharply off from Elasmobranchs, and shows that their skull has reached a much higher stage of development. These bones have the form of richly sculptured plates and shields, and are developed partly from the mucous membrane lining the mouth and covering the visceral skeleton, and partly from the skin covering the roof of the skull, where the arrangement of the bones (*e.g.* frontals and parietals) typical of higher forms can to some extent be recognised. A narrow parasphenoid forms a roof to the oral cavity. The operculum is more pronounced than in the Holocephali, and is also supported by bones (cf. p. 90). The whole palato-mandibular apparatus—which is comparatively small,

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[1] A small basimandibular element has been described in Læmargus, and mandibular rays can be recognised in the primitive Pleuracanthidæ from the Permian formation.

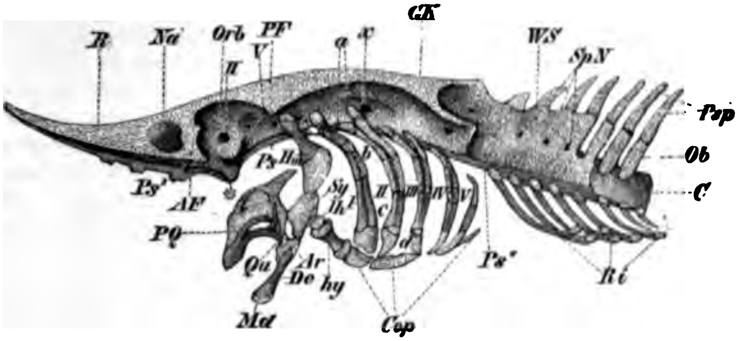

FIG. 67.—CRANIAL SKELETON OF STURGEON (*Acipenser*) AFTER REMOVAL OF THE EXOSKELETAL PARTS.

Ar, articular; *C*, notochord; *Cop*, basal elements of the visceral skeleton; *De*, dentary; *GK*, auditory capsule; *Hm*, hyomandibular; *hy*, hyoid; *I* to *V*, first to fifth branchial arches, with their segments the double pharyngobranchial (*a*), the epibranchial (*b*), the ceratobranchial (*c*), and the hypobranchial (*d*); *Ih*, interhyal; *II*, optic foramen; *Md*, mandible; *Na*, nasal cavity; *Ob*, neural arches; *Orb*, orbit; *PF*, *AF*, postorbital and antorbital processes; *PQ*, palatoquadrate; *Ps*, *Ps'*, *Ps"*, parasphenoid; *Psp*, neural spines; *Qu*, quadrate; *R*, rostrum; *Ri*, ribs; *SpN*, apertures for spinal nerves; *Sy*, symplectic; *WS*. vertebral column; *x*, vagus foramen; *, prominent ridge on the basis cranii.

bears no teeth, and in relation with which bones are formed is connected very loosely with the skull by means of a hyomandibular and symplectic, as well as by ligaments (Fig. 67).

The dermal skeleton attains a much more considerable development in the Bony Ganoids (Crossopterygii and Holostei), and gives rise to a dense armour composed of numerous bones lying on the roof and extending into all parts of the skull and jaws (Fig. 68, A and B): amongst these may be noted a median (Amia) or paired (Polypterus) *jugular plate* between the rami of the mandible. In addition to the investing bones, replacing bones are present in the occipital, otic, orbitotemporal, and ethmoidal regions. Investing and replacing bon [illegible] r to those of Teleosts (p. 92) also occur in connection with the palatoquadrate and the entire visceral skeleton, including Meckel's cartilage and the branchial arches. Though still largely retained, especially in Amia, the cartilage thus becomes relatively reduced as compared with the cartilaginous Ganoids (Fig. 68, B).

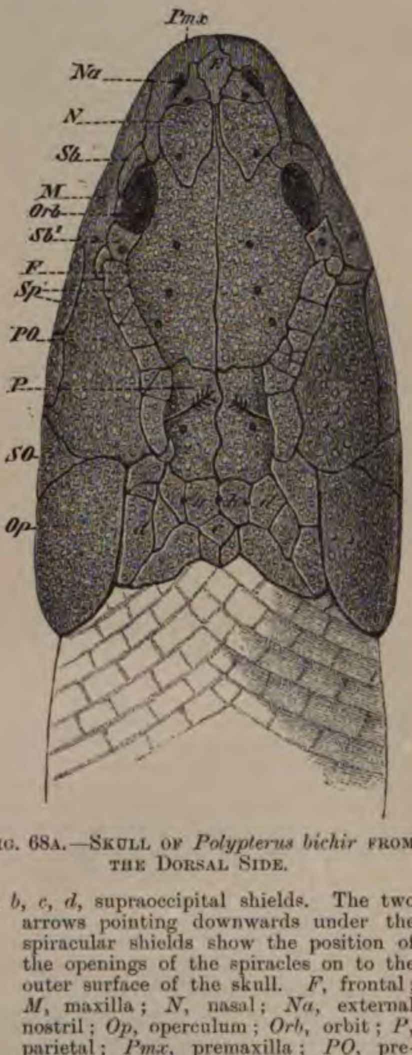

Fig. 68A.—Skull of *Polypterus bichir* from the Dorsal Side.

a, *b*, *c*, *d*, supraoccipital shields. The two arrows pointing downwards under the spiracular shields show the position of the openings of the spiracles on to the outer surface of the skull. *F*, frontal; *M*, maxilla; *N*, nasal; *Na*, external nostril; *Op*, operculum; *Orb*, orbit; *P*, parietal; *Pmx*, premaxilla; *PO*, preoperculum; *Sb*, *Sb'*, anterior and posterior suborbital; *SO*, suboperculum; *Sp*, prespiracular bones.

At the posterior end of the trabeculæ, which only remain separated from one another by a narrow slit, a lateral basipterygoid process arises in Lepidosteus for articulation with the palatoquadrate arch, which is thus connected with the skull not only indirectly, through the hyomandibular, but also directly.

The opercular bones are more highly developed than in cartilaginous Ganoids, and may include an operculum, a preoperculum, a suboperculum, and an interoperculum as well as branchiostegal rays: these in part correspond to investing bones of the cartilaginous hyoid rays. A symplectic, an interoperculum, and branchiostegal rays are wanting in Polypterus.

The branchial skeleton in Ganoids consists of four or five more or less strongly ossified and segmented gill-arches, decreasing in size antero-posteriorly (Fig. 67); in Bony Ganoids the surface which looks towards the throat is beset with teeth.

The Ganoidei are of special interest, as they, with the Elasmobranchii, constitute almost the entire Fish-fauna through the Silurian, Devonian, and Carboniferous periods, and as the Teleostei, which appear later, are doubtless derived from them. They show, moreover, a connection with the Dipnoi and with the oldest Amphibia from the Carboniferous and Trias (Stegocephali).

In the **Teleosts**, the skull (Figs. 69 and 70) presents a large amount of variation; its ground-plan, however, may always be derived from that of the Bony Ganoids, as is best seen by a comparison of the Siluroids with Amia. On the other hand, no relations with the Amphibia are observable, and we must consider the whole group of the bony Fishes as a side branch of the piscine phylum.

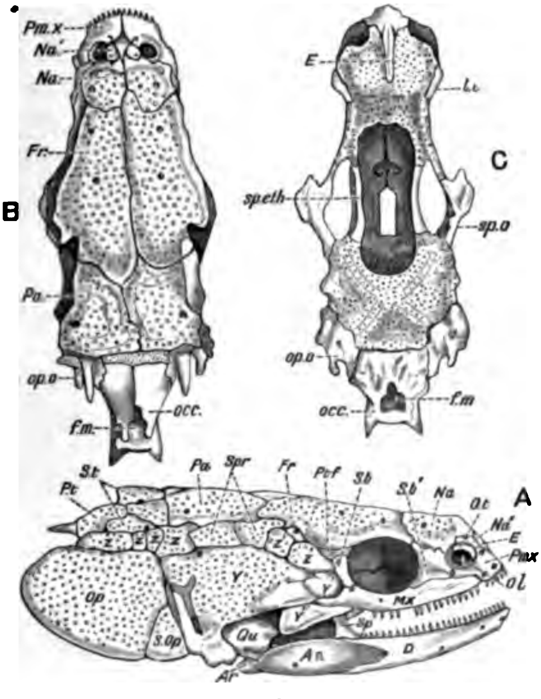

FIG. 68B.—SKULL OF POLYPTERUS. A, LATERAL, AND B AND C DORSAL VIEWS, THE LATTER AFTER REMOVAL OF THE DERMAL BONES, THE CARTILAGE DOTTED. (From Traquair.)

An, angular; *Ar*, articular; *D*, dentary; *E*, mesethmoid; *f.m*, foramen magnum; *Fr*, frontal; *l.e*, lateral ethmoid; *Mx*, maxilla; *Na*, *Na'*, nasal and accessory nasals; *occ*, occipital; *ol*, nasal aperture; *op*, operculum; *op.o*, opisthotic; *O.t*, "os terminale"; *Pa*, parietal; *Pmx*, premaxilla; *P.t*, posttemporal; *Ptf*, postparietal; *Qu*, quadrate; *S.b*, *S.b'*, suborbitals; *S.Op*, sub operculum; *Sp*, splenial; *sp.eth*, "sphenethmoid," in the orbitosphenoid and alisphenoid region, resembling the like-named bone of Amia (*q.v.*); *sp.o*, sphenotic; *Spr*, prespiracular ossicles; *S.t*, supratemporals; *Y*, preoperculum (cheek plate); *Y'*, *Y''*, smaller cheek plates; *z*, postspiracular ossicles; *z'*, prespiracular ossicles.

Much of the cartilaginous primordial skull persists in many

Teleostei (Fig. 70), and in this respect such forms as Argyropelecus and Cyclothone acclinidens deserve special mention. The cranial cavity may reach between the eyes as far as the ethmoidal region, or may become reduced to a narrow cartilaginous and fibrous interorbital septum.

In addition to the general account of the various investing and replacing bones of the skull on pp. 82–84, the following points may

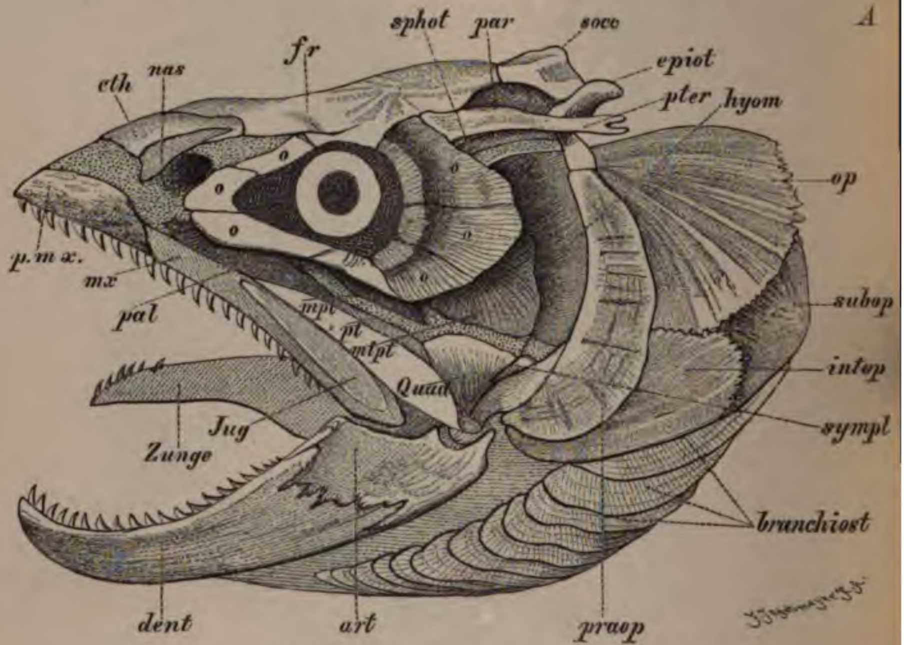

FIG. 69.—CRANIAL SKELETON OF THE SALMON. From the left side.

art, articular; *branchiost*, branchiostegal rays; *dent*, dentary; *epiot*, epiotic; *eth*, supraethmoid; *fr*, frontal; *hyom*, hyomandibular; *intop*, interoperculum; *Jug*, jugal; *mpt*, mesopterygoid; *mtpt*, metapterygoid; *mx*, maxilla; *nas*, nasal; orbital ring; *op*, operculum; *pal*, palatine; *par*, parietal; *P.mx*, premaxilla; *præp*, preoperculum; *pt*, pterygoid; *pter*, pterotic (squamosal); *Quad*, quadrate; *socc*, supraoccipital; *sphot*, sphenotic; *subop*, suboperculum; *Zunge*, tongue.

be mentioned, and the reader is referred to Figs. 69 and 70 for further details.

As in Ganoids, the chief roofing bones of the skull are the parietals and frontals, the former of which may be separated from one another by a process of the supraoccipital. Laterally to the frontal is a sphenotic, which extends backwards to the pterotic (squamosal, cf. p. 83). Supratemporals and jugular plates are never present.

Forming the lateral walls of the skull in the orbital region is

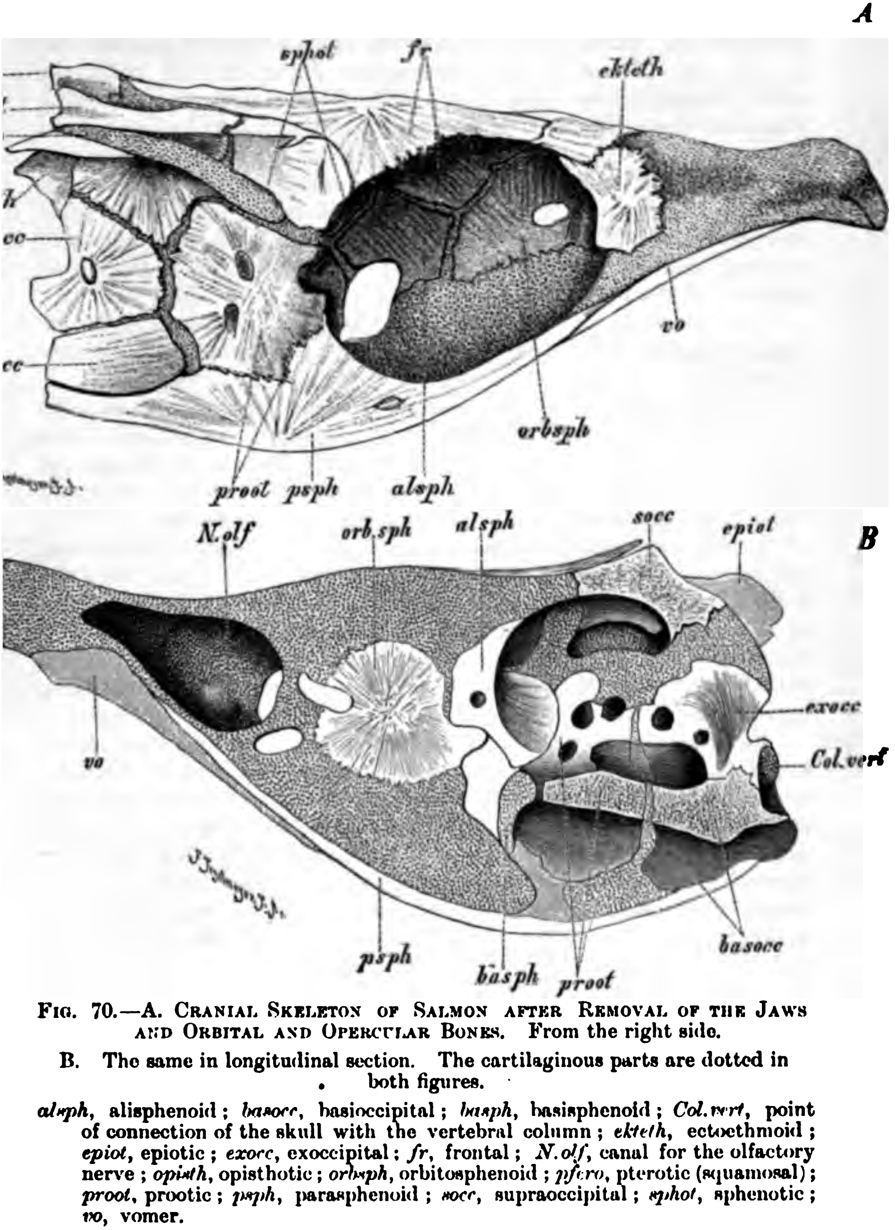

Fig. 70.—A. Cranial Skeleton of Salmon after Removal of the Jaws and Orbital and Opercular Bones. From the right side.

B. The same in longitudinal section. The cartilaginous parts are dotted in both figures.

alsph, alisphenoid; *basocc*, basioccipital; *basph*, basisphenoid; *Col.vert*, point of connection of the skull with the vertebral column; *ekteth*, ectoethmoid; *epiot*, epiotic; *exocc*, exoccipital; *fr*, frontal; *N.olf*, canal for the olfactory nerve; *opisth*, opisthotic; *orbsph*, orbitosphenoid; *ptero*, pterotic (squamosal); *proot*, prootic; *psph*, parasphenoid; *socc*, supraoccipital; *sphot*, sphenotic; *vo*, vomer.

an ossified zone, the anterior and posterior parts of which are usually known respectively as the orbitosphenoid and alisphenoid.

On the base of the skull is a basisphenoid, ventrally to which is a parasphenoid, developed in the mucous membrane of the mouth. More anteriorly is a vomer, and laterally the palatoquadrate bar, which remains separate from its fellow and is connected with the skull-base anteriorly. In connection with the anterior part of this bar the palatine (investing and replacing bone) is formed, and with the posterior part a quadrate. Between these, bony elements are developed which are known as pterygoids, of which may be distinguished a replacing metapterygoid, an entopterygoid, and an investing mesopterygoid or ectopterygoid (cf. pp. 82–84). These bones are already represented in Bony Ganoids, and form, together with the base of the skull, the roof of the oral cavity.

The olfactory sacs are sunk in the ethmoid cartilage, in which region supraethmoid and lateral ethmoid (ectethmoid) bones are developed.

In the auditory region, as in Bony Ganoids, are a prootic, an epiotic, and an opisthotic, the most important of which is the prootic. The opisthotic usually does not form an actual part of the auditory capsule, with which, however, as already mentioned, other bones (pterotic, sphenotic) may come into relation.

In the occipital region, with which vertebral elements are assimilated, are exoccipitals, which largely or entirely surround the occipital foramen, and a basioccipital, as in Bony Ganoids, as well as a very variable supraoccipital, which is wanting in the last-mentioned group (Fig. 68, B). Where the basioccipital is in contact with the vertebral column, it presents a concavity containing notochordal tissue.[1]

Forming the margin of the upper jaw are a premaxilla and a maxilla. These play an important part in all Vertebrates from the Bony Ganoids onwards, but in Teleosts more particularly they show considerable variation with regard to their relative development, form, and arrangement, and in many cases the maxilla takes no part in bounding the actual gape of the mouth, and does not form a continuous bar with the premaxilla. Of the bones in relation with the oral cavity, the vomer, the parasphenoid, the premaxilla, and the maxilla may bear teeth. The maxilla, however is edentulous except in the Physostomi.[2]

Besides the above-mentioned bones in connection with the jaws, the cranial capsule of Teleosts is surrounded by other outworks consisting of bony plates and bars. These arise as true dermal bones in the region of the eyes (*orbital ring*), and in the gill-covers (*opercular bones*): the latter are similar in number and name to those of many Bony Ganoids (p. 90). A large number of

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[1] A curious asymmetry is seen in the head of adult Pleuronectidæ. When hatched, these Fishes are quite symmetrical, but later on the eye of one side becomes rotated, so that eventually both eyes are situated on the same side; in consequence of this, the skull also becomes asymmetrical. In many Teleosts a canal, lying in the axis of the base of the skull, encloses the eye-muscles, and opens on either side into the orbits.

[2] The tactile barbules present on the head of many Fishes, (*e.g.*, Siluroids) are supported by skeletal parts (cf. p. 82.)

branchiostegal rays are developed in the ventral parts of the opercular fold or branchiostegal membrane (Fig. 69).

Anteriorly, the opercular apparatus lies against a bony chain consisting of three pieces—the hyomandibular, symplectic, and quadrate—which serves as a suspensorial apparatus for the lower jaw (Fig. 69). The latter consists of Meckel's cartilage and of several bony elements, the largest of which is the toothed dentary: the others are the articular, angular, and coronary. The last two, however, may be wanting. The articular is developed in the articular portion of Meckel's cartilage, which latter is ensheathed by the dentary and angular.

The hyoid arch is usually followed by four branchial arches and a rudimentary fifth which forms the "inferior pharyngeal bone." The dorsal segments of these arches become fused together to form the "superior pharyngeal bone," which, like the inferior pharyngeal, usually bears teeth.

The skull of **Dipnoans** is in a sense intermediate between that of Chimæroids and Teleostomes on the one hand, and that of Amphibians (more especially Urodeles) on the other. In various respects, however, it presents special characters, such as the marked metameric segmentation of the occipital region and the relations of certain of the investing bones.

The chondrocranium is retained almost entirely in the most primitive existing representative of this group—Ceratodus, and to a large extent in the other two genera: the only perichondral bones being a pair of exoccipitals (Fig. 71). The occipital region is firmly connected with the vertebral axis, and the two or three anterior vertebral elements which are united with the skull may possess more or less distinct neural arches and spines (*e.g.* Protopterus): the vagus nerve passes through a space between the auditory capsule and first neural arch.[1] A large "cranial rib" articulates with the hinder part of the skull on either side, in a position corresponding to the third occipital neural arch.

The cranial cavity extends forwards between the orbits to the ethmoidal region (platybasic type), and its front wall (*lamina cribrosa*) is largely cartilaginous. The cartilaginous nasal capsules are lattice-like, and as in all Vertebrates higher in the scale, each nasal cavity communicates with the mouth by internal nostrils: the external nostrils are covered by the upper lip.[2]

The ethmo-nasal region is covered by a median dermal supra-ethmoid, postero-laterally to which is a supraorbital bony lamella ("dermal lateral ethmoid"), and articulating with it posteriorly in the median line in Ceratodus is another unpaired bony lamella

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[1] In the embryo of Ceratodus it has been shown that there are five myotomes anterior to this point.

[2] There are two so-called "labial cartilages," one of which arises from the trabecular region, passing behind and to the outer side of the external nostril, and the other probably belongs to the nasal skeleton.

("scleroparietal"). The last mentioned element is wanting in the other two genera, in which an unpaired frontoparietal covers the roof and part of the side walls of the chondrocranium, on the ventral side of which is a large parasphenoid.

The squamosal is closely applied to the solid palatoquadrate cartilage, which becomes fused with the cranium (autostylic type), and in connection with which a palatopterygoid bone is present. A premaxillo-maxillary arch is wanting.

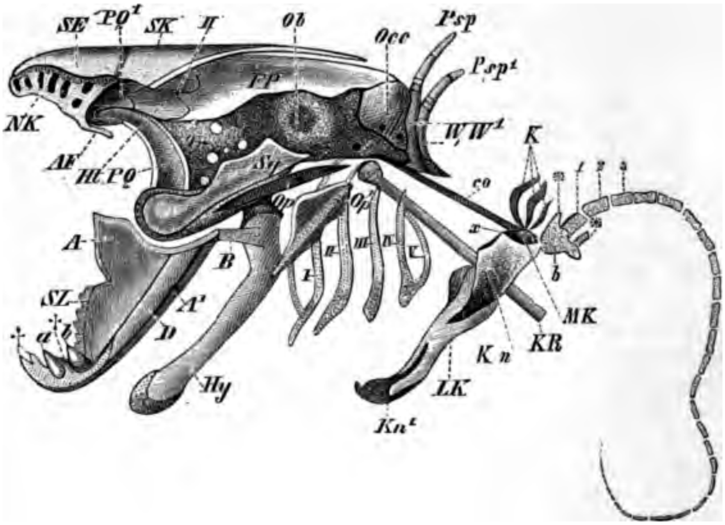

FIG. 71.—SKULL, WITH THE PECTORAL ARCH AND FIN, OF PROTOPTERUS.

A, splenial; *AF*, antorbital process (the labial cartilage in this region is not indicated); *a*, *b*, *SL*, teeth; *B*, *co*, fibrous bands; *D*, angular, *FP*, frontoparietal; *Ht*, membranous fontanelle, perforated by the optic foramen (II); *Hy*, ceratohyoid; *KR*, cranial rib; *Kn*, coraco-scapular cartilage; *LK*, clavicle; *MK*, supraclavicle; *NK*, fenestrated cartilaginous nasal capsule; *Ob*, auditory capsule; *Occ*, exoccipital, with the hypoglossal foramina; *Op*, operculum; *Op'*, interoperculum, overlying cartilaginous vestiges of hyoid rays; *PQ*, palatopterygoid, which converges towards its fellow at *PQ'*; *SE*, dermal supraethmoid; *SK*, supraorbital (dermal lateral ethmoid); *Sq*, squamosal, overlying the quadrate cartilage; *Tr*, palatoquadrate cartilage; *W*, *W'*, vertebral elements with their neural spines (*Psp*) united with the skull; *x*, facet on the pectoral arch for articulation with the basal segment (*b*) of the fin; **, vestigial lateral rays on the basal segment of the fin; 1—3, the three following segments: ††, projections of Meckel's cartilage; I—V, branchial arches: I and II are segmented (concerning the bar arising from I anteriorly, cf. note on p. 97).

The strong lower jaw is ossified by an angular and a splenial, and in Ceratodus a dentary is also present. Meckel's cartilage extends freely for a short distance anteriorly.

The teeth, which are sharp and blade-like, are borne on the palatopterygoid and mandible; small "vomerine" teeth are also present, though there is no actual vomer.

The hyoid arch consists on either side of a large ceratohyal, and in Ceratodus a small hyomandibular and hypohyal, as well as a median basihyal, are also present. The five branchial arches[1] are comparatively small and weak, and some, or even all of them, may be entirely unsegmented (Lepidosiren).

The Dipnoi constitute a very ancient group, which must have diverged from the main piscine stem at a very early period, for they occur in the Trias and Carboniferous, and even extend into the Devonian and possibly into the Silurian.

Amphibians.

Urodela.—The skull of tailed Amphibians is distinguished from that of bony Fishes in general principally by negative characters,—on the one hand by the presence of less cartilage in the adult, and on the other by a reduction in the number of bones (Fig. 72). In brief, its structure is in many respects simpler, and becomes modified in adaptation to the different mode of life. Moreover, no nerve-apertures are present in the occipital region behind that for the vagus; but as this region extends to a slight extent posteriorly to the vagus foramen, it appears that a reduction has here taken place. The occipital part of the skull has the form of a neural arch, united with the auditory capsules above and broadening out below where it abuts against the notochord, forming a basal plate primarily including vertebral elements, on the posterior surface of which are two occipital condyles, as in all other Amphibians (Figs. 60 and 72). An exoccipital bone is developed on either side.

The platybasic cranium is not laterally compressed in the orbital region, and the brain, flanked by the cartilaginous and bony cranial walls, extends between the orbits as far as the olfactory capsules, at which point the cranial cavity is closed by a membranous (Triton) or cartilaginous (Salamandra) ethmoid region (*lamina cribrosa*), perforated by the olfactory nerves, or in certain cases by special modifications of the frontal bones (Proteus, Salamandra perspicillata). The anterior part of the lateral cranial walls may be ossified as an orbitosphenoid. The well-developed auditory capsules are connected with one another dorsally by a narrow cartilaginous bar (*tectum synoticum*)—all that remains of such an extensive cartilaginous roof as is seen in Elasmobranchs: this is retained in all the higher Vertebrates. In the ossification of the capsules the prootics take the chief part, and later unite with the exoccipitals. A new and important modification as compared with Fishes is the presence of an aperture, the *fenestra ovalis*, s. *vestibuli*, on the outer and lower side of each capsule, and corresponding to part of the original space between the capsule and the parachordal cartilage. This fenestra is closed by a cartilaginous plug, the *stapedial plate*, which is connected with the quadrate and paraquadrate (see p. 82) by ligament, or by a cartilage or bone (*columella auris*), the two structures probably together corresponding phylogenetically to the upper section of the hyoid arch (hyomandibular), though this homology can no longer be traced ontogenetically. The olfactory capsules are well developed and arise in part independently and partly in connection with the converging trabeculæ. In Necturus and Proteus they are delicate and fenestrated, and united with the cranium by connective tissues only.

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[1] In Protopterus, a delicate cartilaginous rod arises from the first branchial arch (Fig. 71), concerning the homology of which opinions differ. It may represent the first branchial arch (and in this case the number of branchial arches is six); or it may belong to the hyoid arch, thus indicating that the latter is primarily double; or, again, it may possibly correspond to a branchiostegal ray.

The snout is limited anteriorly by the toothed premaxillæ, which usually more or less completely enclose a cavity (intermaxillary or internasal sinus) containing a gland. Each external nostril is bounded by the nasal process of the premaxilla, the nasal, and the toothed maxilla, and a small investing bone, the septomaxillary, is also present between the maxilla and nasal in relation with the nostril. The premaxillæ and maxillæ form the upper boundary of the gape. Between the nasal and maxilla is a prefrontal, and medially to this a frontal, followed behind by a parietal, which partly covers the auditory capsules.

Forming the greater part of the skeletal roof of the oral cavity and strengthening the skull-base is a large and broad parasphenoid (Fig. 72), which, as in Fishes, is sometimes provided with teeth. It extends forwards from the occipital region to the olfactory capsules, closing over the basicranial fontanelle, and ventral to it is the paired and toothed vomero-palatine bar, the two elements comprising each of which become fused in adult Urodeles, but vary much in form and arrangement. The vomerine part of this bar is situated beneath the olfactory capsule and is in contact with the premaxilla and maxilla, thus helping to strengthen this region, at the posterior part of which is the internal nostril, situated much more posteriorly than in Dipnoans. Internally to the suspensorium is a pterygoid bone, a process of which extends forward towards the maxilla.

The suspensorium is much more simple than that of Fishes (Figs. 72 and 73). It consists of the palatoquadrate only, with a quadrate ossification, and has usually four typical processes connecting it with surrounding parts (pedicle or basal process, otic, ascending, and pterygoid processes). The quadrate[1] becomes fused secondarily with the skull, and on its outer surface is an investing

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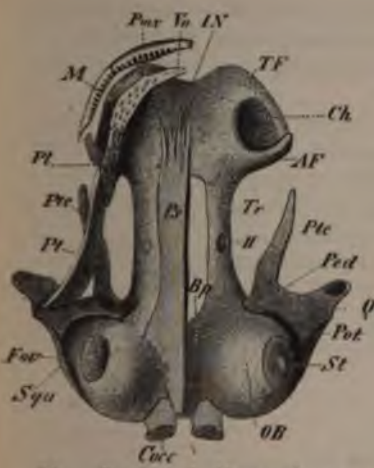
[1] In *Tylototriton verrucosus* the quadrate sends forwards a process which connects it with the maxilla, and thus forms a lower zygomatic arch or infra-temporal arcade.



72A.—SKULL OF A YOUNG AXOLOTL (*Amblystoma*). Ventral view.

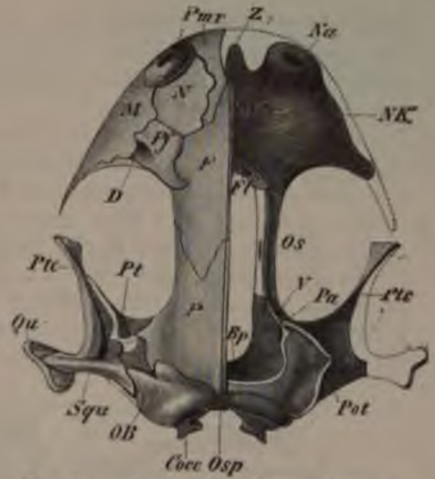


FIG. 72B.—SKULL OF *Salamandra atra* (ADULT). Dorsal view.

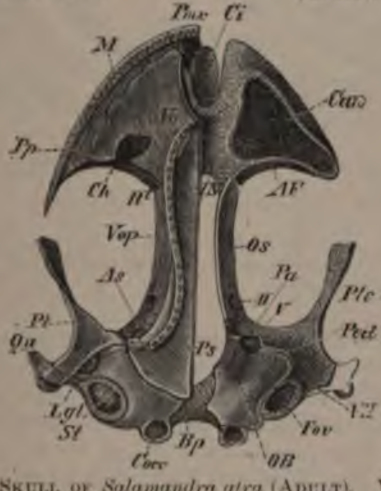


FIG. 72C.—SKULL OF *Salamandra atra* (ADULT). Ventral view.

As, posterior part of "alisphenoid" region; *Bp*, cartilaginous basal plate between the auditory capsules; *Can*, nasal cavity; *Cocc*, occipital condyles; *F*, frontal; *Fl*, foramen for the olfactory nerve; *Fov*, fenestra ovalis, closed on one side by the stapedial plate (*St*); *IN*, internasal plate, which extends laterally to form processes (*TF* and *AF*) bounding the internal nostrils (*Ch*); *Lgt*, ligament between the stapes and suspensorium; *M*, maxilla; *N*, nasal; *Na*, external nostrils; *NK*, nasal capsule; *OB*, auditory capsule and exoccipital; *Os*, orbitosphenoid; *Osp*, tectum synoticum; *P*, parietal; *Pf*, prefrontal, perforated at *D* for the lacrymal duct; *Pl*, palatine; *Pmx*, premaxilla; *Pot*, otic process, *PED*, pedicle, and *Pa*, ascending process of the quadrate; *Pp*, palatine process of maxilla; *Ps*, parasphenoid; *Pt*, bony pterygoid; *Ptc*, cartilaginous pterygoid; *Qu*, quadrate; *Rt*, point of entrance of the ophthalmic branch of the fifth nerve into the nasal capsule; *Squ*, paraquadrate ("squamosal"); *Tr*, trabecula; *Vo*, vomer; *Vop*, vomeropalatine; *Z*, tongue-like outgrowth of the internasal plate, which forms a roof for the internasal cavity; *II*, optic, *V*, trigeminal, and *VII*, facial foramina.

bone, the *paraquadrate* (Gaupp), usually described as a squamosal. The quadrate, exoccipital, prootic, orbitosphenoid, and columella arise in the perichondrium and are replacing bones, while all the others are investing bones.

The temporal region is either uncovered by skeletal parts, or an *upper zygomatic bar* (*supratemporal arcade*) is formed by processes of the paraquadrate and frontal respectively, and indicates a reduction of a more marked development of bone in this region such as occurred in the Stegocephali.

In connection with the lower jaw are usually developed a replacing articular at the proximal end of Meckel's cartilage, and investing splenial and dentary bones. The rest of the visceral skeleton of Urodeles undergoes various modifications in the different types. We may consider the ground-form, as exhibited in the larva, to consist of five pairs of bars in addition to the mandibular arch (Fig. 73), in which latter the palatoquadrate and Meckel's cartilage chondrify independently. The anterior bar, or hyoid, consists of two pieces (Fig. 74, A), as do also the two first branchial arches. The third and fourth branchial arches are much smaller, and even vestigial in Salamanders. All these bars are connected with a single or double basal piece. At the close of larval life, that is, when the gills are lost, the two hinder pairs of arches disappear entirely, while the two anterior pairs undergo changes as regards form and position,[1] and may become more or less densely ossified (Fig. 74, B—D).

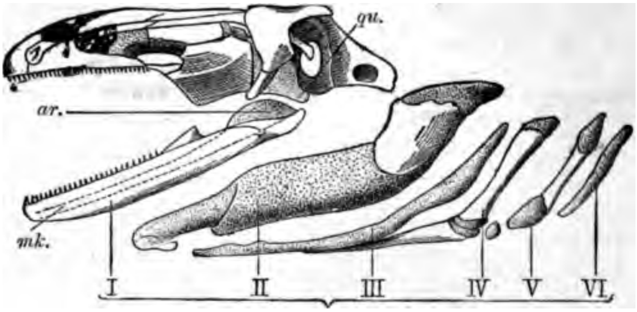


FIG. 73.—SKULL AND VISCERAL ARCHES OF *Menopoma*. From the side.

I, mandible; II, hyoid; III-VI, branchial arches; *qu*, quadrate, covering which is the paraquadrate ("squamosal"); *ar*, articular; *mk*, Meckel's cartilage enclosed by the dentary bone.

Gymnophiona.—In contrast to the extensive and compact chondrocranium of most Urodela and of Anura, that of the limbless Amphibians consists of delicate cartilaginous rods separated by wide spaces; and even where connected sheets of cartilage are present, they are very delicate and thin. At the same time the skull nearly resembles that of Urodeles (more especially perennibranchiate forms) in spite of a considerable reduction in its parts—especially in the occipital, auditory, and orbital regions, as well as of the peculiar and characteristic

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[1] In the genus Spelerpes, which possesses a sling-like tongue, the dorsal segment of the first branchial arch grows out into a long cartilaginous filament, which extends far back under the dorsal integument (Fig. 74, D).

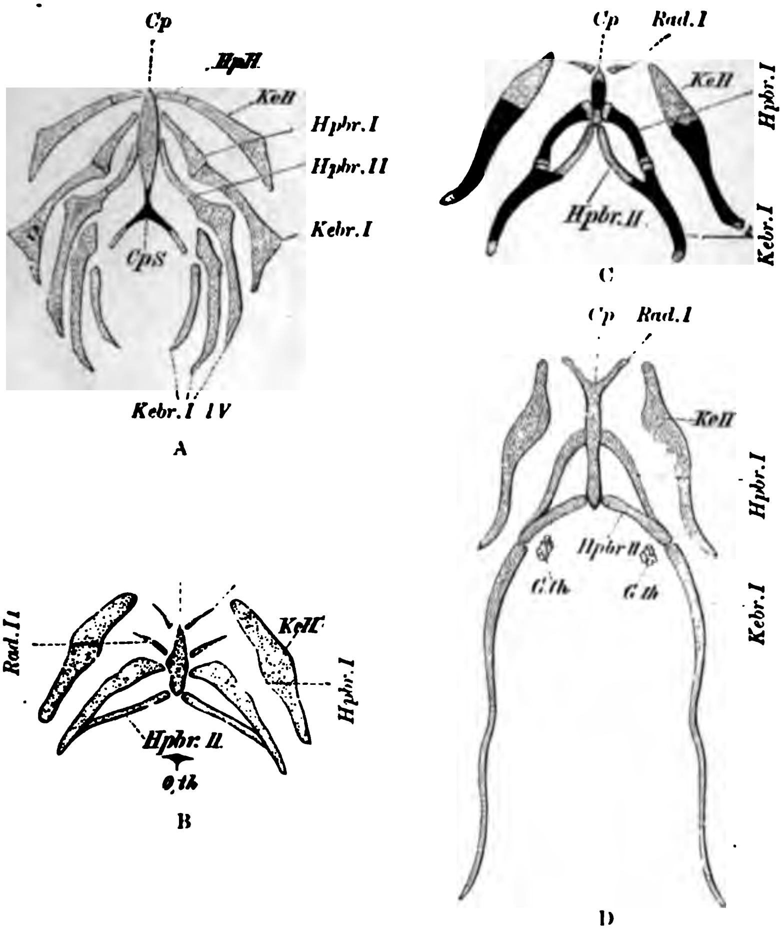

FIG. 74.—HYOBRANCHIAL APPARATUS OF URODELES. A, Axolotl (*Siredon* stage of *Amblystoma*); B, *Salamandra maculosa*; C, *Triton cristatus*; D, *Spelerpes fuscus*.

Cp, *Cps*, *O.th*, basihyobranchial or copula; *G.th*, thyroid gland; *Hpbr. I* and *II*, first and second hypobranchial; *HpII*, *Rad I*, hypohyal; *Kebr. I–IV*, first to fourth ceratobranchial; *KeII*, ceratohyal ("anterior cornu" of hyoid in Caducibranchs—the "posterior cornu" being made up of *Hpbr I* and *II* and *Kebr I*). *Rad. II* arises in Salamandra secondarily during metamorphosis.

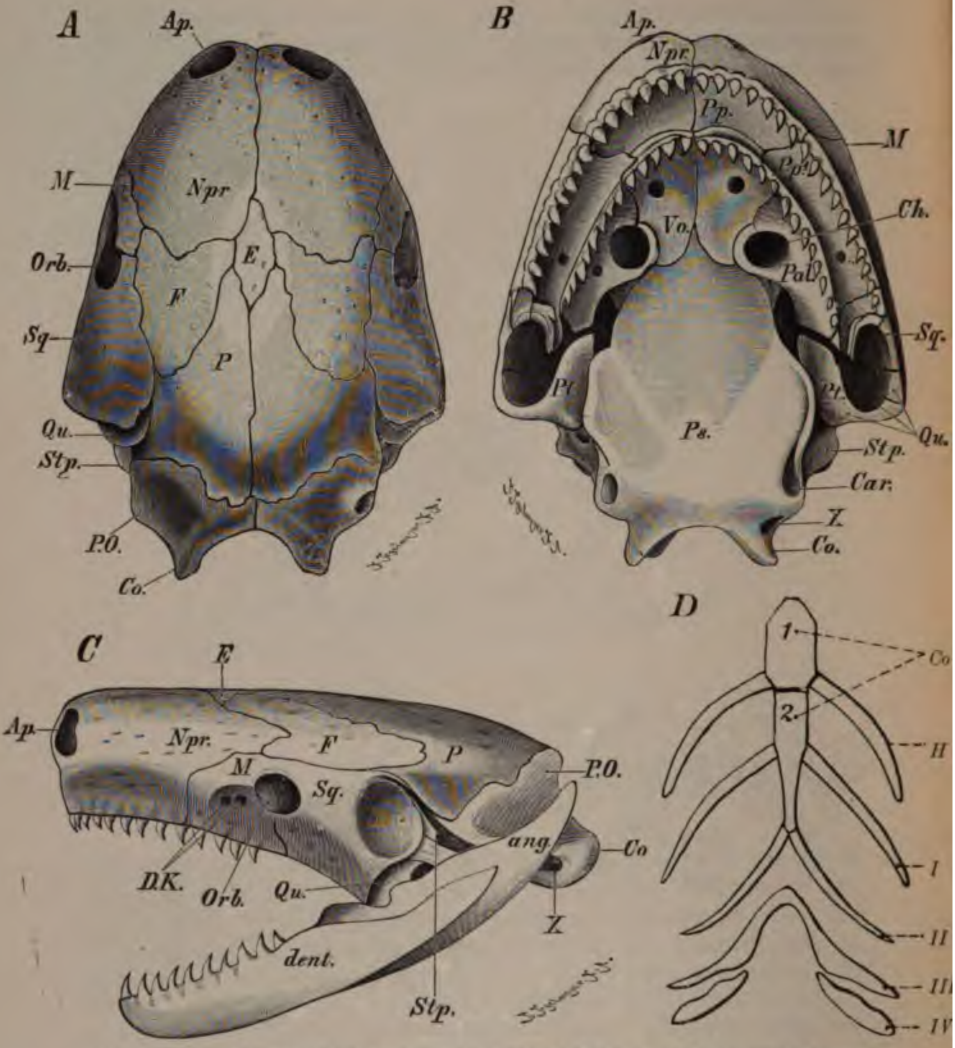

FIG. 75.—A, DORSAL, B, VENTRAL, C, LATERAL VIEW OF SKULL OF *Siphonops annulatus*.

Ap, external nostril; *ang*, angular; *Car*, carotid foramen; *Ch*, internal nostril; *Co*, occipital condyle: *dent*, dentary; *DK*, apertures for ducts of tentacular gland; *E*, ethmoid region; *F*, frontal; *M*, maxilla; *Npr*, naso-premaxilla; *Orb*, orbit; *Pal*, palatine; *Po*, petroso-occipital; *Pp*, *Pp′*, palatine process of the naso-premaxilla and of the maxilla; *Ps*, parasphenoid, united posteriorly with the auditory and occipital elements; *Pt*, pterygoid; *Qu*, quadrate; *Sq*, paraquadrate ("squamosal"); *Stp*, stapedial plate; *Vo*, vomer; *X*, vagus foramen.

D, Hyobranchial apparatus of the larva of *Ichthyophis glutinosa*. After P. and F. Sarasin.); *Co* 1, 2, first and second basal elements (copulæ); *H*, hyoid; I—IV, branchial arches.

solidarity of the osteocranium, doubtless due to adaptation in connection with the burrowing habits of this group (Fig. 75). The differences are due essentially to the more extensive ossification, and to the fusion of certain of the bones, *e.g.* the parasphenoid, otic, and occipital elements, and the premaxilla and nasal. The temporal region, moreover, is more or less covered by bone, and the ethmoid skeleton is well developed, the solid nasal septum enclosing no gland.

The post-mandibular visceral skeleton consists in the larva, as in that of Urodeles, of a hyoid and of four branchial arches which, however, have a more primitive and piscine form and arrangement and are less reduced than in Urodeles (Fig. 75, D). In the adult, the median basal connection between the first and second branchial arches disappears, and the vestige of the fourth arch unites with its predecessor.

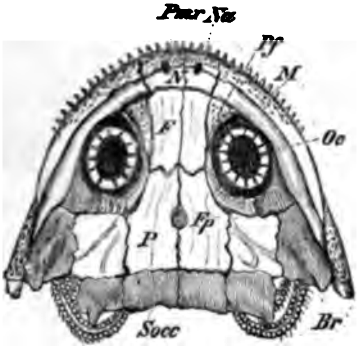

FIG. 76.—RESTORATION OF THE SKULL OF A SMALL STEGOCEPHALAN (PROTRITON) from the Carboniferous of Bohemia. (After Fritsch.)

Br, branchial apparatus; *F*, frontal; *Fp*, parietal foramen; *M*, maxilla; *N*, nasal; *Na*, nostril; *Oc*, sclerotic ring (orbital bones); *P*, parietal; *Pf*, prefrontal; *Pmx*, premaxilla; *Socc*, supraoccipital.

The skull of the fossil **Stegocephali**, some of which were comparatively gigantic, was covered by a much larger number of dense and firm bony shields, and a foramen was present in the parietal region, which, like that in modern Lizards, is in relation to the pineal apparatus (Fig. 76). A row of bony sclerotic plates was usually present around the orbit like those of Birds and certain recent and fossil Reptiles (*e.g.* Lizards, Ichthyosaurus). Many of these forms possessed the same number of visceral arches as Urodeles, and it has been shown that they (*e.g.* Branchiosaurus) underwent a metamorphosis.

The class Amphibia, like the Reptilia, was of much greater importance in earlier periods of the earth's history than at present, but existing forms cannot be traced directly to those of the Carboniferous and Permian strata.

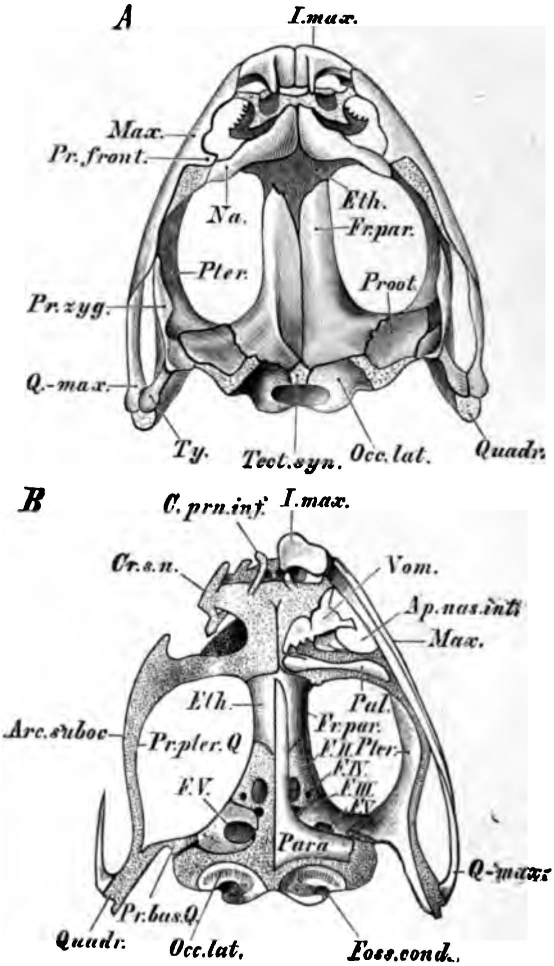

FIG. 77.—A and B. Dorsal and Ventral Views of the Skull of *Rana esculenta* (× 2). In B the Investing Bones are removed on the Right Side.

Ap.nas.int, internal nostril; *Arc.suboc*, subocular or palatopterygoid arch; *C.prn.inf*, inferior prenasal cartilage; *Cr.s.n*, subnasal crest; ***Eth***, sphenethmoid; *F II—V*, foramina for cerebral nerves; *Foss.cond*, condyloid fossa, in which are the foramina for the IXth and Xth cerebral nerves; *Fr.par*, frontoparietal; *I.max*, premaxilla; *Max*, maxilla; *Na*, nasal; *Occ.lat*, exoccipital; *Pal*, palatine; *Para*, parasphenoid; *Pr.front*, frontal process of maxilla; *Proot*, prootic; *Pr.zyg*, zygomatic process of paraquadrate; *Pr.bas.Q*, basal process of quadrate; *Pr.pter.Q*, pterygoid process of quadrate; *Pter*, pterygoid; *Q max*, quadratojugal (or quadratomaxilla); *Quadr*, quadrate; *Tect.syn*, tectum synoticum; *Ty*, paraquadrate ("squamosal"); *Vom*, vomer.

Anura.—The skull of adult tailless Batrachia is at first sight very similar to that of Urodeles: it is platybasic, and the occipital region has the same morphological value. It undergoes, however, especially in the parts surrounding the gape, an essentially different and much more complicated development, and cannot in any way be directly derived from that of tailed Amphibians, so that the common ancestral form must be sought in very early geological periods. The chondrocranium (Figs. 77 and 78) is much more extensive than in Urodeles, and is largely retained in the adult, the bones not gaining the upper hand to such an extent.

The larva, or tadpole, in adaptation to the nature of its food and mode of feeding, possesses a suctorial mouth, provided with labial cartilages and horny jaws and denticles. The articulation of the lower jaw with the palatoquadrate is situated very far forwards, and at metamorphosis becomes shifted backwards, thus causing a considerable widening of the gape of the mouth.

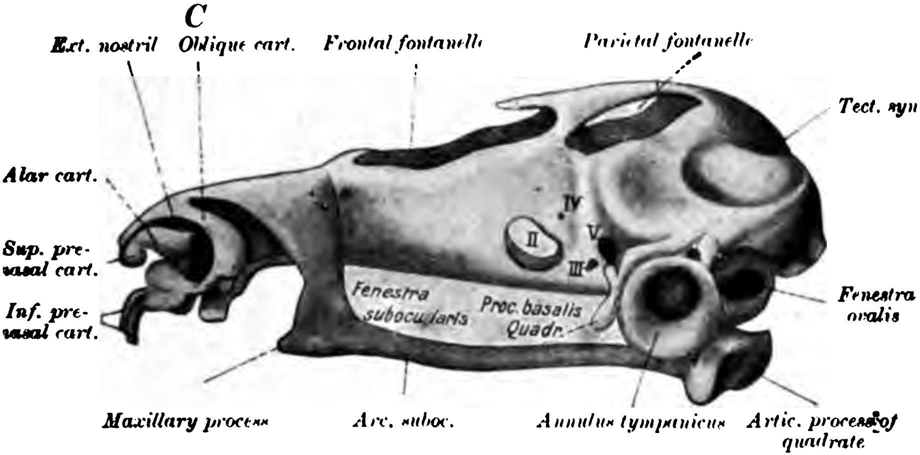

FIG. 77, C.

LATERAL VIEW OF A WAX MODEL, RECONSTRUCTED FROM SECTIONS, OF THE CHONDROCRANIUM OF A YOUNG *Rana temporaria*, ABOUT 2 CM. LONG. The Stapedial Plate and Columella are removed, and the Ossifications are not indicated. (After Gaupp.)

An important advance on other Amphibia is seen amongst Anura (*e.g.* Ranidæ) in connection with the auditory organ. The first visceral (hyomandibular or spiracular) cleft disappears entirely during development in the Urodela and Gymnophiona, but becomes modified in many Anura to form a *Eustachian tube*, opening into the pharynx and leading into a *tympanic cavity*. The latter is closed externally by a tympanic membrane supported by a cartilaginous ring (*annulus tympanicus*,[1] Figs. 77, *C*, and 78), and to it the distal end of the columella (p. 98) is attached.

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[1] Cf. under Auditory Organ. The tympanic ring is a derivative of the palatoquadrate.

On the dorsal side of the chondrocranium are a large median anterior fontanelle or fenestra, and a smaller paired posterior fontanelle, and the cartilage becomes replaced by bones in the occipital, auditory, and ethmoid regions (Figs. 77 and 78). There are paired exoccipital and prootics and a sphenethmoid, the lateral parts of which correspond in position to the orbitosphenoids of Urodeles, and which encircles the whole skull; it also forms a front wall to the cranial capsule, perforated by the olfactory nerves.

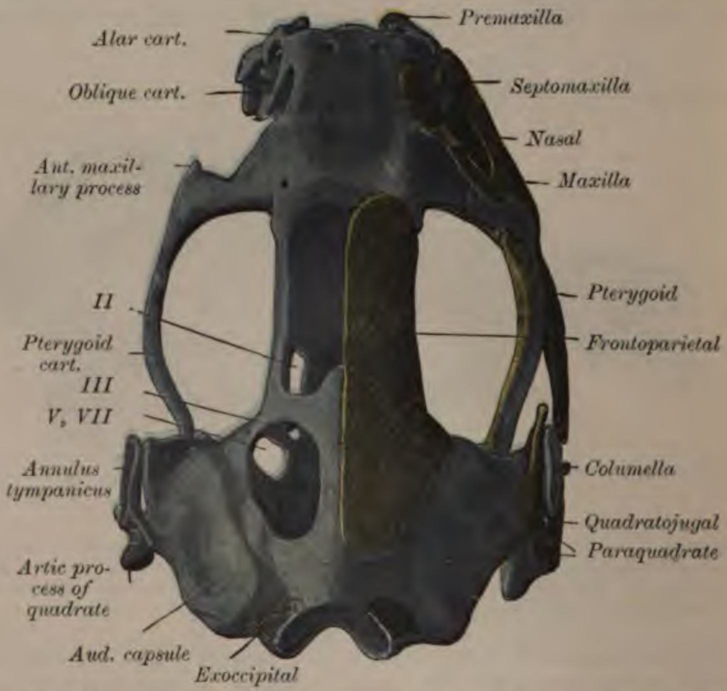

Fig. 78.—Skull of a Young *Rana temporaria*, 2 cm. in Length, just after Metamorphosis, from the Dorsal Side. The Investing Bones are removed on the Left Side (× abt. 11.) After Gaupp, from a model by Fr. Ziegler.)

Cartilage—*blue*; replacing bones—*gray*; investing bones—*yellow*.

The frontal and parietal of either side are as a rule fused, thus giving rise to a frontoparietal. The maxillary bar grows backwards much further than in Urodeles, and becomes connected with the suspensorium by means of a small intermediate bone, the quadratojugal, or quadratomaxilla (Figs. 77 and 78). There is thus a *lower zygomatic arch* (cf. p. 98); an upper zygoma like that of many Urodeles is never developed, and consequently the temporal region is uncovered by skeletal parts. The palatoquadrate is united anteriorly with the cartilaginous nasal capsule this is characteristic for the Anura (except Ranodon) as compared with the Urodela. (For the relations of the bones bounding the mouth-cavity, cf. Figs. 77, A and B).[1]

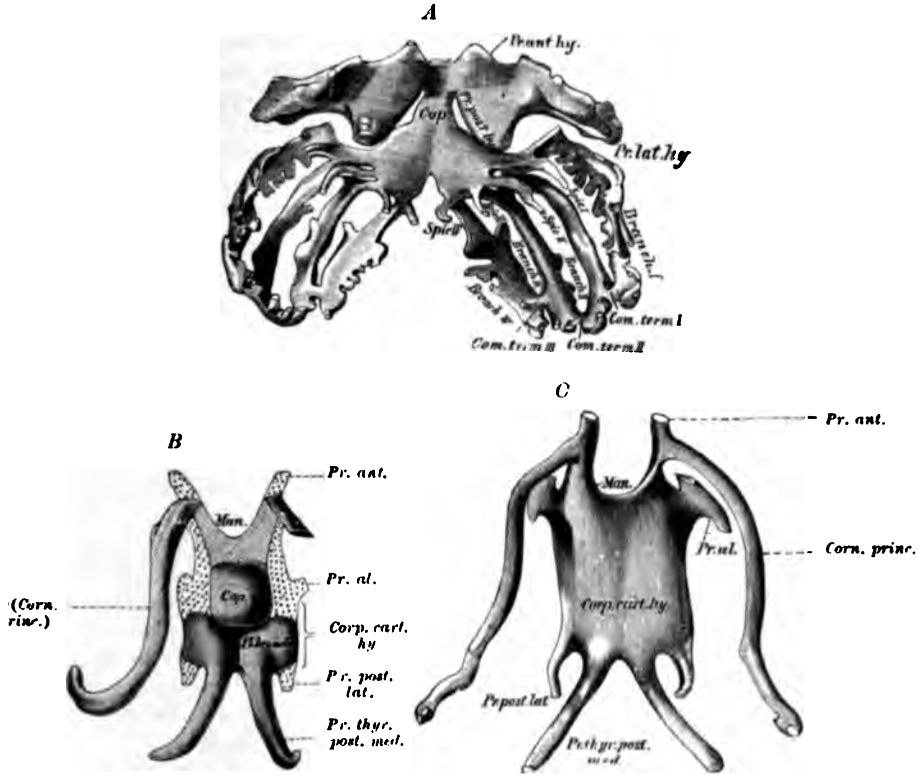

FIG. 79.—A. HYOBRANCHIAL SKELETON OF A LARVAL *Rana temporaria*, 29 MM. IN LENGTH, FROM THE DORSAL SIDE. B. THE SAME OF A LARVA, 15 MM. IN LENGTH, AT THE END OF METAMORPHOSIS, AFTER DISAPPEARANCE OF THE TAIL. C. HYOID CARTILAGE OF A YOUNG FROG, 2 CM. IN LENGTH, FROM THE VENTRAL SIDE.

(All these figures are from wax models after Gaupp.)

A and B (in part), *Branch I—IV*, branchial arches ; *Com. term. I -III*, terminal commissures of same ; *Cop*, basal plate (copula) ; *Hy*, hyoid ; *Pr.ant.hy*, *Pr.lat.hy*, *Pr.post.hy*, anterior, lateral, and posterior processes of the hyoid ; *Spic. I—IV*, cartilaginous processes.

B (in part) and C. *Corp.cart.hy*, body of hyoid cartilage: *Corn princ*, anterior cornu ; ***Man***, "manubrium" ; *Pr.al*, alary process ; *Pr.ant*, anterior process ; *Pr.post.lat*, postero-lateral process ; *Pr.thyr.post.med*, thyroid or postero-medial process (posterior cornu.)

The bones of the lower jaw are a dentary and an angular (or angulosplenial). At the distal end of Meckel's cartilage a small portion ("lower labial cartilage" of larva) is bent inwards towards the median line and unites with its fellow in a symphysis, forming in the adult the mentomandibular (p. 84).

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[1] A septomaxillary, helping to close the nasal fenestra on the outer side, is present, as in Urodeles (p. 98).

There is a much greater reduction of the branchial skeleton at the close of larval life than in Urodeles. In the larva, representatives of the hyoid and of four branchial arches can be recognised, but these are all united together and form a continuous structure (Fig. 79, A). The greater part of the broad basal parts of this apparatus, as well as the four branchial arches, disappear during metamorphosis. The hyoid cartilage of the adult (B, C) is formed partly from the remains of the hyobranchial cartilages of the larva and partly by new outgrowths from it.

Reptiles.

The skull in Reptiles is extremely complex and varied as regards its bones and their relations. Although differing markedly in many important respects from the cranial skeleton of Amphibians, the ground-form of the latter is distinctly recognisable, especially in the primitive Hatteria and in Lizards. On the other hand, numerous points of similarity are seen in the skull, as well as many other parts, of Reptiles and Birds, which are, therefore, included together under the term *Sauropsida.*

In spite, however, of the similarity of plan of the amphibian and reptilian skull, it must be borne in mind that no recent Amphibian lies on the direct line of descent of the Reptiles, though certain fossil Amphibians (Stegocephali) and Reptiles, as well as the existing Hatteria, help to bridge over the space between the two Classes.

In order not to cause confusion by reference to the multifarious details which present themselves in dealing with the reptilian skull, it will be as well to consider first its more important characteristics, many of which are common to the Amniota in general, before treating specially of the various Orders. In this general description, the lacertilian skull will be chiefly referred to as a typical form (Figs. 80 and 82).

Apart from its naso-ethmoidal region, the chondrocranium plays no important part in Reptiles subsequently to the embryonic period, and it no longer forms such a complete structure as, *e.g.*, in Anura, but is considerably reduced and frequently largely fenestrated (Fig. 80). This want of completeness, however, is later partly compensated for by the investing bones, and as the ossification is very considerable, a firm and solid skull results.

The cranium includes three more vertebral elements than in Amphibia (p. 97), so that the foramina for the three roots of the compound hypoglossal nerve perforate the skull. In all Amniota the cranio-vertebral boundary is in a similar relative position, in spite of differences of form in this region. The cerebro-nasal axis, which is horizontal in Amphibians, becomes more or less bent

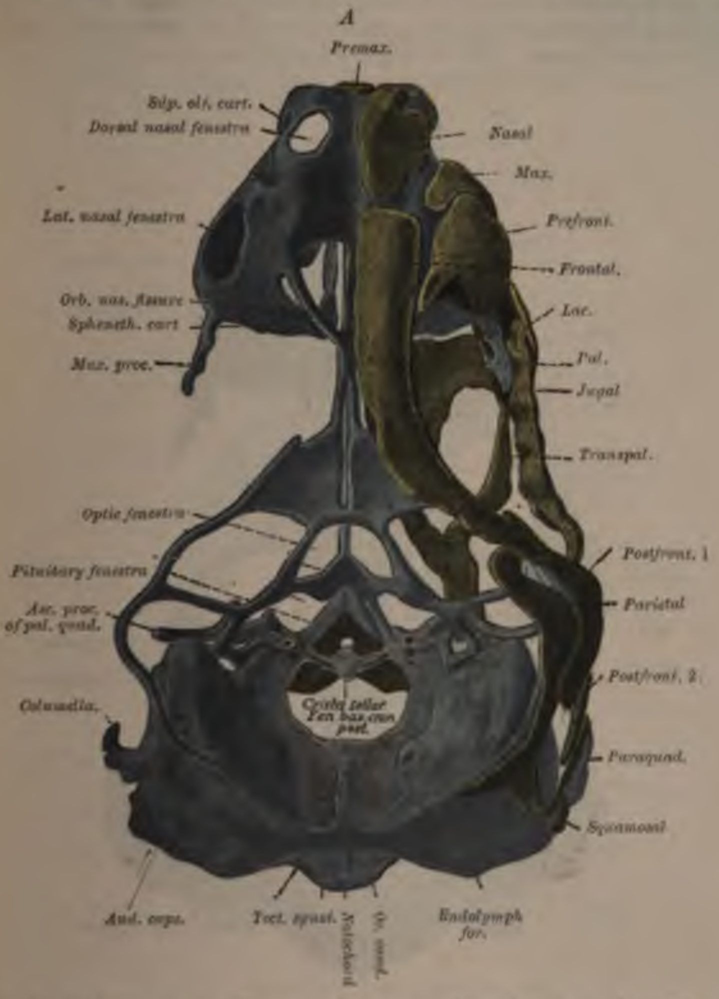

FIG. 80.—SKULL OF AN EMBRYO *Lacerta agilis*, 47 MM. IN LENGTH. A, DORSAL, AND B, VENTRAL VIEW. C, LOWER JAW AND HYOBRANCHIAL SKELETON, FROM THE VENTRAL SIDE.

(After Gaupp, from a wax model by Ziegler × ⅛.) Cartilage, *blue*; replacing bones, *gray*; investing bones, *yellow*.

downwards in front of the interorbital region, and thus causes various modifications as regards the relations of the nasal and cranial cavities (cf. Fig. 90).

The cranial bones (Figs. 80–86) are much more numerous and varied in form than in recent Amphibia. The solid base of the skull is formed by bones developed on a cartilaginous foundation, viz., of a basioccipital and a basisphenoid, on which latter there may be a *basipterygoid process* on either side for articulation with the pterygoid bone. An alisphenoid ossification may be present; presphenoids and orbitosphenoids are usually wanting. The parasphenoid, which plays so important a part in the Anamnia as an investing bone on the roof of the mouth, undergoes a gradual reduction, but can still be recognised, although more or less included within the basisphenoid: it may be represented by *basitemporal* ossifications which unite with the latter bone, and its anterior part may form a *basisphenoidal rostrum*. Above the

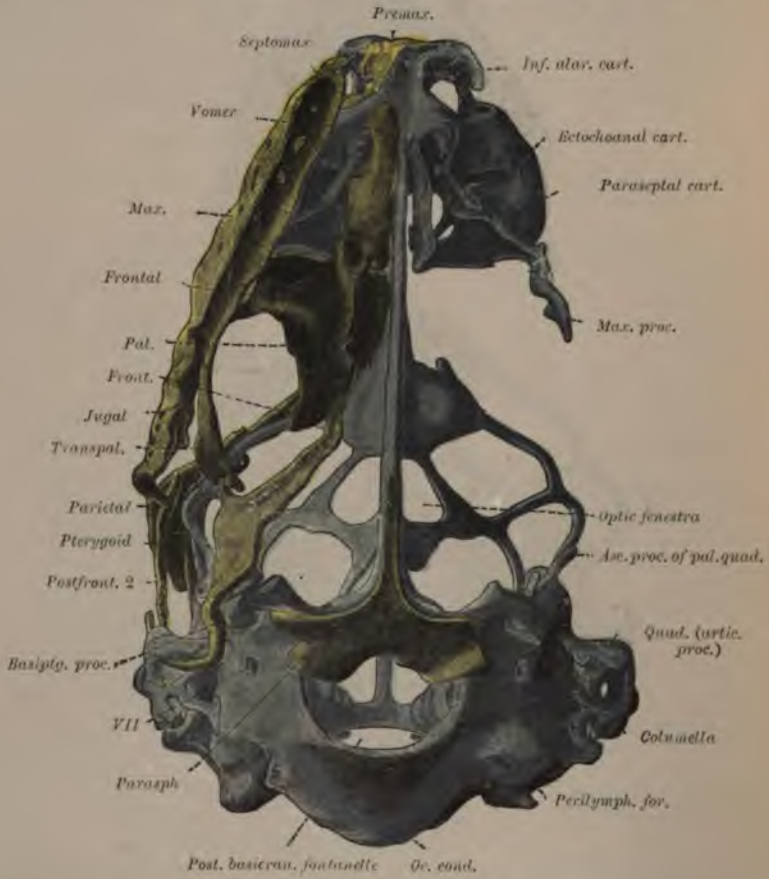

FIG. 80, *B.*

basioccipital are a pair of exoccipitals, and above these again a supraoccipital, which arises in the cartilage of this region (*tectum synoticum*, cf. p. 97). In contradistinction to the Amphibia, only a *single* condyle connects the skull with the vertebral column in the Sauropsida: this, on close examination, is usually seen to be formed of three parts, derived from the basioccipital and exoccipitals respectively.

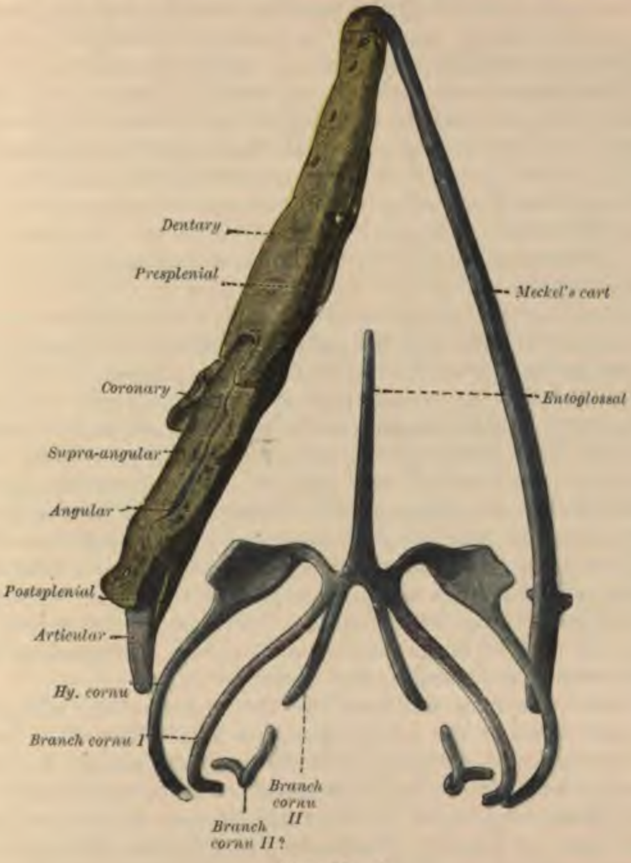

FIG. 80, C.

The auditory capsules are ossified from three centres, the most important of which, as in Amphibians, is the prootic, which usually remains free, the epiotic uniting with the supraoccipital and the opisthotic with the exoccipital. A *fenestra rotunda* is present in the walls of the capsule in addition to a fenestra ovalis, into which latter the stapedial plate of the bony columella is inserted (cf. p. 98), and the tympanic cavity in most Reptiles communicates with the pharynx by means of a Eustachian tube.[1]

In most Reptiles a fibro-cartilaginous interorbital system is present (tropibasic character, p. 77), but there is much variation in its development, and the anterior part of the cranial cavity tends to become more or less reduced and shifted dorsalwards.

On the roof of the skull the parietals usually, and the frontals sometimes, are fused together: a median so-called "parietal foramen" (under Brain) is present in certain recent and fossil forms. The frontals and parietals are either confined to the skull roof, or may also take part in forming its lateral walls. Prefrontals and postfrontals are also present, and there may be a postorbital in addition, as well as a series of supraorbital bones posteriorly to the prefrontal and laterally to the frontal, forming the upper margin of the orbit. Anteriorly to the frontals are, in most cases, a pair of nasals, and laterally to the largely cartilaginous ethmoid region, the lacrymals.

Anteriorly to the basisphenoid is a paired or unpaired vomer, postero-laterally to which is the palatine, followed by a pterygoid, which may articulate with the basipterygoid process of the basisphenoid. Connecting each pterygoid and maxilla in most Reptiles is a so-called *transpalatine* or *ectopterygoid*, and in certain forms a rod-like *epipterygoid* (or *antipterygoid*) extends in a vertical direction between the parietal and pterygoid, and is comparable to the ascending process of the quadrate in Urodeles.

The premaxillæ, which are in many cases fused together, come into contact with the nasals dorsally and the maxilla laterally: the latter usually bounds the greater part of the gape. A septomaxillary (p. 98) may be present. Teeth occur in nearly all Reptiles, and may be borne on the palatine and pterygoid, as well as on the premaxilla, maxilla, and dentary.

The quadrate may be fixed to the surrounding bones, or movably articulated: the pterygopalatine bar is frequently more or less movable and free from the base of the skull. In some Reptiles its elements become broadened out, and, together with a shelf-like palatine process of the maxilla, may in certain cases even take part in forming a secondary roof to the oral cavity, or *hard palate*, distinct from the true (sphenoidal) base of the skull. Thus the vomer becomes cut off from the cavity of the mouth and forms a vertical plate situated above the hard palate, and the internal nostrils are thrown further back.

In the temporal region, typical differences are seen in the various Orders which indicate a very early divergence from the common reptilian ancestor. The bones in this region may form a series of bars, or *arcades*, separated by spaces or *fossæ*. The main temporal fossa is usually separated [illegible] from the postfrontal or post[illegible] further subdivided into [illegible] of bone, the *upper zyg*[illegible] by processes of the postfrontal [illegible] The jugal may be connected with [illegible] jugal or paraquadrate [illegible] *inferior temporal arcade*.

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[1] The form of the columella varies considerably: it consists primarily of a bony rod, to which a cartilaginous *extrastapedial* is attached distally and applied to the tympanic membrane: both parts are derivatives of the hyoid.

In the nomenclature of [illegible] Reptiles much confusion exists. According to Gaupp all Crocodiles, Chelonians, Lizards, and most Snakes possess a squamosal, all Crocodiles and almost all Chelonians and Lizards a paraquadrate (cf. p. 82), but none of the above possesses a quadrato-jugal (quadrato-maxillary). In Hatteria the latter is present united with the well developed paraquadrate, while the squamosal appears to be entirely wanting. In narrow-mouthed Snakes all three of these elements are absent.

A number of bones arise in connection with the lower jaw which includes remains of Meckel's cartilage; viz., a dentary, angular, supra-angular, splenial, coronary, and articular.

Thus it will be seen that the number of investing bones in the reptilian skull is very considerable, and it may be convenient to enumerate them in this place:—parietal, frontal, nasal, squamosal, prefrontal, septomaxillary, postorbital, jugal and quadratojugal, lacrymal, paraquadrate, parasphenoid, premaxilla, maxilla, vomer, palatine, pterygoid, transpalatine, dentary, angular, supra-angular, splenial, and coronary. In addition to these integral and typical elements, a number of less constant accessory bones occur in many forms (*e.g.* among Lizards) (*e.g.* supraorbitals, supraoculars, supratemporals); they arise as ossifications in the derm comparatively late.

In consequence of the absence of branchial respiration during development, the hyobranchial apparatus plays a less important part in Reptiles than in the Anamnia and [illegible] reduction, in some cases only traces of it remaining.

The chief points characteristic of the [illegible] Orders of Reptiles are enumerated below [illegible] the reader is referred to Figs. 80–86.

Rhynchocephali. In Hatteria (Fig. 81) [illegible]

The squamosal and paraquadrate [illegible] tion of upper and lower [illegible] arcades (cf. p. 106) [illegible] types may be [illegible] Amphibia [illegible] nephrona, Stegocephala [illegible] *zygokrotaphic* [illegible] with lower zygomatic [illegible] Tritonidæ, most Lacertilia [illegible] zygomatic arches—T[illegible] dilia; 3 [illegible] all Ophidia, some Lacertilia [illegible] orbital septum is present. The frontals and parietals are paired, and there is a parietal foramen. *Three* bony arcades are seen in the temporal region—a superior, an inferior, and a posterior. The quadrate is large, and is firmly fixed to the skull by means of the

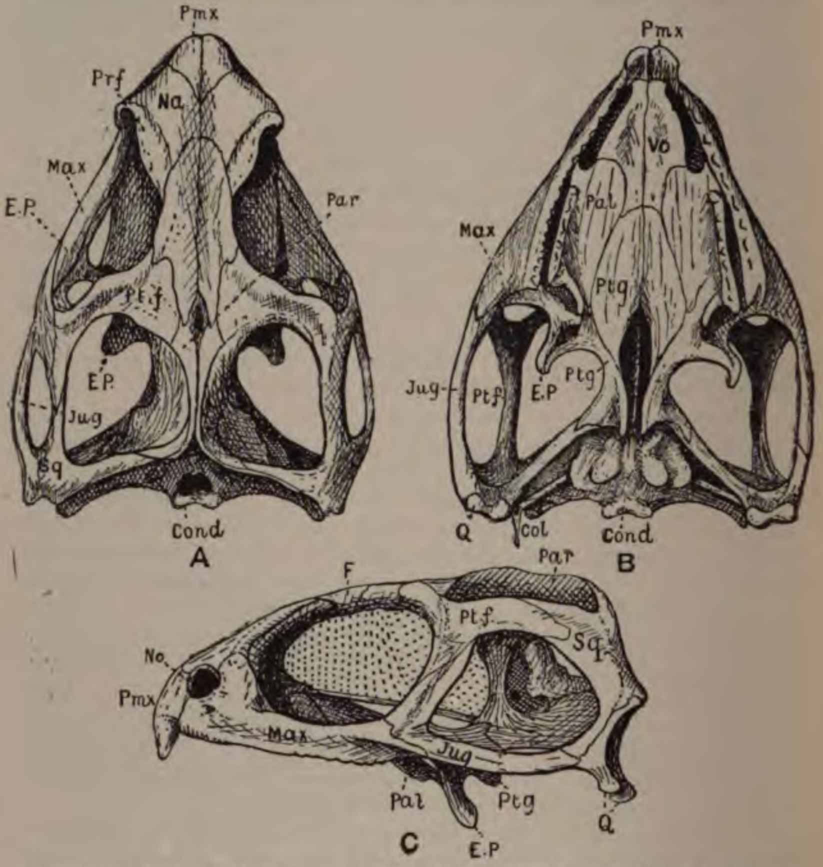

FIG. 81.—SKULL OF HATTERIA. A, dorsal; B, ventral; and C, lateral view, $\times \frac{2}{3}$. (From Gadow, Cambridge Natural History.)

col, columella auris; *Cond*, occipital condyle; *E.P*, transpalatine or ectopterygoid; *F*, frontal; *Jug*, jugal; *Max*, maxilla; *Na*, nasal; *No*, external nostrils; *Pal*, palatine; *Par*, parietal; *Pmx*, premaxilla; *Prf*, prefrontal; *Pt.f*, postfrontal and postorbital; *Ptg*, pterygoid or endopterygoid; *Q*, quadrate and quadrato-jugal; *Sq*, paraquadrate (squamosal); *Vo*, vomer.

quadratojugal, pterygoid, paraquadrate ("squamosal"), and exoccipital. The vomers, palatines, and pterygoids are broadened out and form a bony roof to the mouth. An epipterygoid is present. The premaxillæ are separated by a suture. Teeth are borne on the maxilla and palatine, as well as on the premaxilla

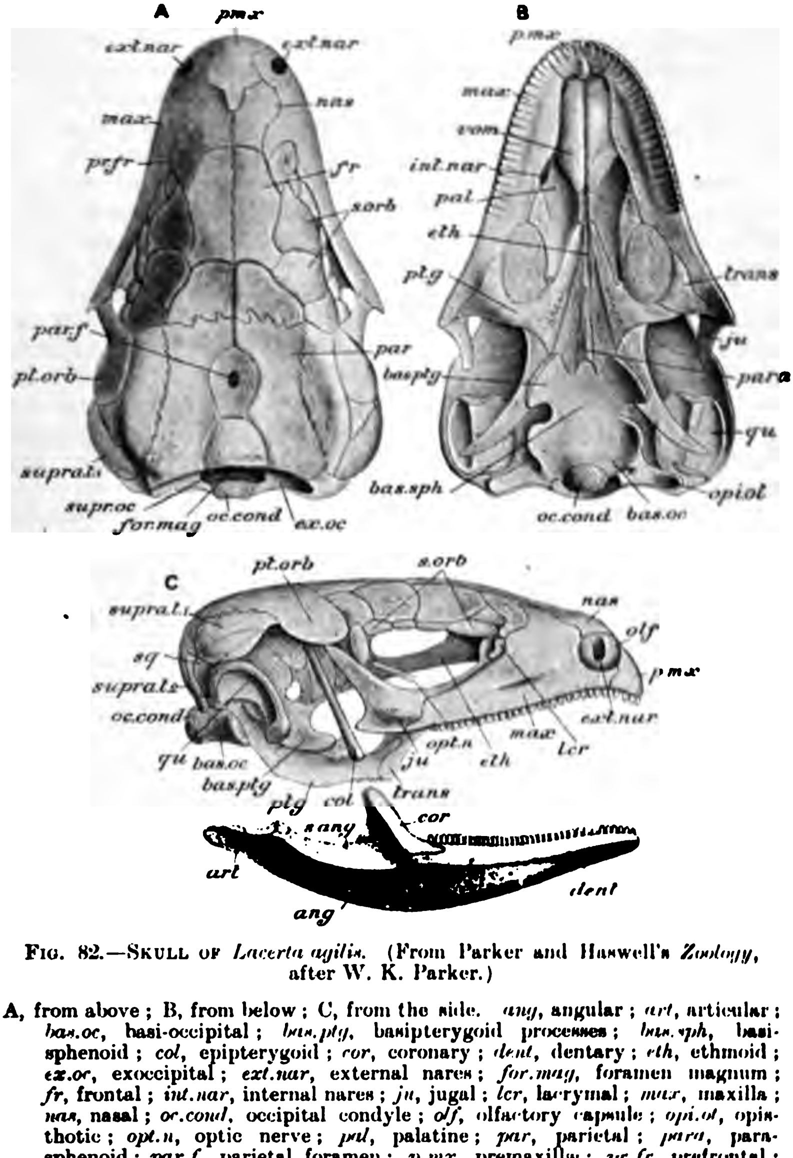

FIG. 82.—SKULL OF *Lacerta agilis*. (From Parker and Haswell's *Zoology*, after W. K. Parker.)

A, from above; B, from below; C, from the side. *ang*, angular; *art*, articular; *bas.oc*, basi-occipital; *bas.ptg*, basipterygoid processes; *bas.sph*, basi-sphenoid; *col*, epipterygoid; *cor*, coronary; *dent*, dentary; *eth*, ethmoid; *ex.oc*, exoccipital; *ext.nar*, external nares; *for.mag*, foramen magnum; *fr*, frontal; *int.nar*, internal nares; *ju*, jugal; *lcr*, lacrymal; *max*, maxilla; *nas*, nasal; *oc.cond*, occipital condyle; *olf*, olfactory capsule; *opi.ot*, opisthotic; *opt.n*, optic nerve; *pal*, palatine; *par*, parietal; *para*, parasphenoid; *par.f*, parietal foramen; *p.mx*, premaxillæ; *pr.fr*, prefrontal; *ptg*, pterygoid; *pt.orb*, postorbital; *qu*, quadrate; *s.ang*, supra-angular; *s.orb*, supraorbitals; *sq*, paraquadrate ("squamosal"); *supra.oc*, supra-occipital; *supra.t.*^{1}, supratemporal; *supra.t.*^{2}, squamosal ("supratemporal^2"); *trans*, transpalatine; *vom*, vomer.

and vomer in young stages. The two dentaries are united by ligament. The columella is continuous with the anterior cornu of the hyoid, the latter consisting of a body (basi-hyobranchial) and of two pairs of cornua.

Lacertilia (Figs. 80 and 82).—There is an interorbital septum except in the Amphisbænidæ, and in it there may be indications of orbitosphenoids or alisphenoids: the orbit is usually separated from the temporal fossa. Various modifications are seen as regards the temporal arcades, but an inferior arcade, or lower zygoma, is never present.[1] The quadrate is in most cases movably articulated to the distal end of a parotic process from the temporal region. There is a "parietal foramen" (situated in the frontal region in Chameleons); the parietals are usually fused, and the frontals may also become united in the adult. Lacrymals are generally present, and epipterygoids occur except, *e.g.* in Amphisbænians and Chameleons. The pterygoid is movably articulated to the quadrate and basipterygoid process of the basisphenoid, and there is a basisphenoidal rostrum. The premaxillæ are usually fused. Teeth occur on the premaxilla, maxilla, dentary, and frequently also on the palatine.

The hyobranchial skeleton (Fig. 80, C) consists of a narrow basal portion extending forwards into the tongue, from which three pairs of cornua may arise, belonging respectively to the hyoid and branchial arches 1 and 2.

Ophidia (Fig. 83).—The embryonic chondrocranium is much less extensive than in Lizards. In the orbito-temporal region there is hardly any cartilage, the parietals and frontals forming lateral walls to the cranium, which extends to the ethmoid region, and even here the amount of cartilage is small. The trabeculæ remain separate for the greater part of their length, forming narrow rods lying side by side, which in many cases can be recognised even in the adult. The skull, however, is here also of the tropibasic type (p. 77): a thin interorbital septum is developed, but is comparatively little marked and does not become chondrified. There is a large parasphenoidal rostrum on the basisphenoid, the parietals are united, and there are no temporal arcades or supratemporal bones. The great strength and solidity of the investing bones is doubtless correlated with the modifications of the jaws in connection with the mode of feeding.

In most Snakes, the quadrate is only indirectly connected with the skull by means of the squamosal, with the distal end of which it articulates and which extends backwards, thus resulting in a very wide gape; moreover, the facial bones are capable of movement upon one another and upon the cranium. The pterygoid articulates posteriorly with the quadrate without the intervention of a jugal. The premaxilla is unpaired and usually edentulous (except, *e.g.* in Pythons). The rami of the mandible are connected by an elastic ligament. Teeth are usually present on the relatively short maxilla, the palatine, pterygoid, and dentary. The hyobranchial apparatus is much reduced, and consists merely of a pair of cartilaginous rods situated beneath the trachea.

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[1] In Chameleons, characteristic processes arise from the cranial roof and temporal regions, and unite above the posterior part of the skull in the median line.

In Viperine Snakes the maxillopalatine apparatus is particularly mobile, and the very short maxilla is articulated with the prefrontal and can swing forward in order to erect the fang. In the burrowing Typhlopidæ, on the other hand, amongst other characters in which they differ from the majority of Snakes, the facial bones are immovably connected with the cranium, and there is no transpalatine.

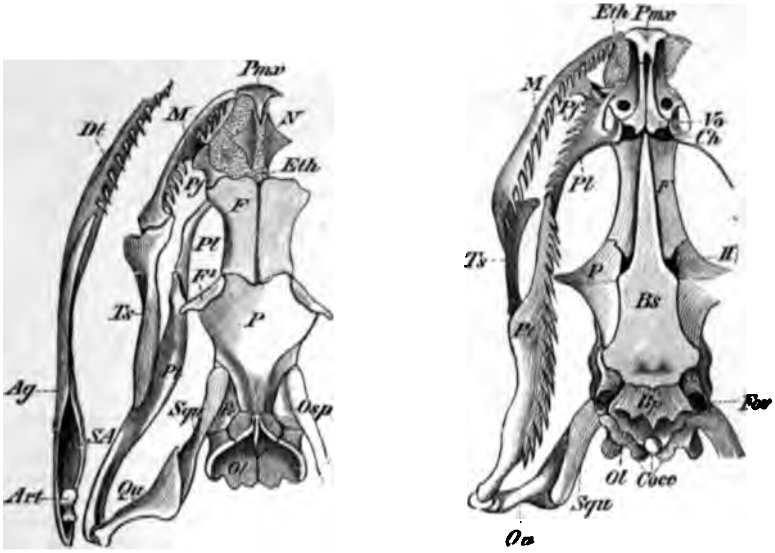

FIG. 83.—SKULL OF COLUBRINE SNAKE (*Tropidonotus natrix*), dorsal and ventral views.

Ag, angular; *Art*, articular; *Bp*, basioccipital; *Bs*, basisphenoid; *Ch*, internal nostrils; *Cocc*, occipital condyle; *Dt*, dentary; *Eth*, ethmoid; *F*, frontal; *F*¹, postorbital; *For*, fenestra ovalis; *II*, optic foramen; *M*, maxilla; *N*, nasal; *Ol*, exoccipital; *Osp*, supraoccipital; *P*, parietal; *Pe*, periotic; *Pf*, prefrontal; *Pl*, palatine; *Pmx*, premaxilla; *Pt*, pterygoid; *Qu*, quadrate; *SA*, supra-angular; *Squ*, squamosal; *Ts*, transpalatine; *Vo*, vomer.

Chelonia (Fig. 84).—The chondrocranium essentially resembles that of Lizards and Crocodiles, and much of the naso-ethmoidal cartilage persists. There is a large supraoccipital crest and usually a lower temporal arcade or jugal arch, except in certain cases where the paraquadrate ("quadrato-jugal") is wanting. The nearly vertical quadrate, which is grooved posteriorly for the columella auris, is very firmly united with the neighbouring bones, and above it is a squamosal. There are no separate nasals or lacrymals, their position being taken by a "prefrontal." The parietals do not unite. The orbit is completely surrounded by bones, and in some forms (*e.g.* Chelone, Sphargis) the whole temporal region is covered by an additional roof, above the cranial roof proper, formed by the parietal, squamosal, and postfrontal. An ossification between the pterygoid and a descending lamella of the parietal (which latter bone forms part of the wall of the cranial cavity) apparently represents an epipterygoid. The palatines give rise to palatine plates, which together with lateral parts of the median vomer help in forming a short hard-palate. The opisthotic remains distinct from the exoccipital, and the premaxilla is usually paired, while the dentaries are united at the symphysis. No indications of a parasphenoid are known, and a transpalatine is wanting.

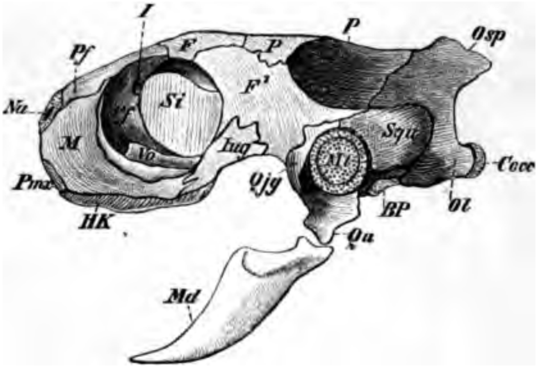

FIG. 84.—SKULL OF YOUNG WATER-TORTOISE (*Emys europæa*). Side view.

BP, cartilaginous interval between basioccipital and basisphenoid; F^1, postfrontal; *HK*, horny sheaths of jaws; *I*, point of entrance of the olfactory nerve into the nasal capsule; *Jug*, jugal; *Md*, mandible; *Mt*, tympanic membrane; *Na*, external nostril; *Osp*, supraoccipital, which gives rise to a crest; *Pf*, prefrontal, which forms a great part of the anterior boundary of the orbit; *Qjg*, paraquadrate ("quadrato-jugal"); *Si*, interorbital septum. Other letters as in Fig. 83.

There are no teeth, which are replaced functionally by horny beaks, as was also the case in certain fossil Reptiles (*e.g.* Ceratopsidæ).

The hyobranchial skeleton is comparatively large, and consists of a body, very closely related to the larynx and produced anteriorly into a short lingual process, of a pair of small hyoid cornua, and of two pairs of larger cornua belonging to the first and second branchial arches (Fig. 85).

Crocodilia (Fig. 86).—The chondrocranium is less fenestrated than in Lizards, and a basipterygoid process is not strongly marked: the interorbital septum, which is inserted vertically between the anterior parts of the trabeculæ, attains a considerable development. Alisphenoids are present.

The bones are very massive and firmly united together by sutures: those on the dorsal and lateral regions are pitted.

The parietals and frontals are unpaired in the adult, and lacrymals, prefrontals, and postfrontals are present. There is an upper and a lower temporal arcade or zygomatic arch, and between the orbit and temporal fossa is a bony pillar formed by the postfrontal, jugal, and transpalatine: the vomer is paired. The palatines and pterygoids are very firmly attached to the base of the skull, and both these bones, as well as the paired premaxillæ and maxillæ, take part in the formation of the hard palate.[1] Thus the internal nostrils open far back, beneath the basioccipital, from which alone the occipital condyle is formed. The exoccipitals meet above the foramen magnum, thus shutting out the supraoccipital. Teeth are present in sockets on the premaxillæ, maxillæ, and dentaries.

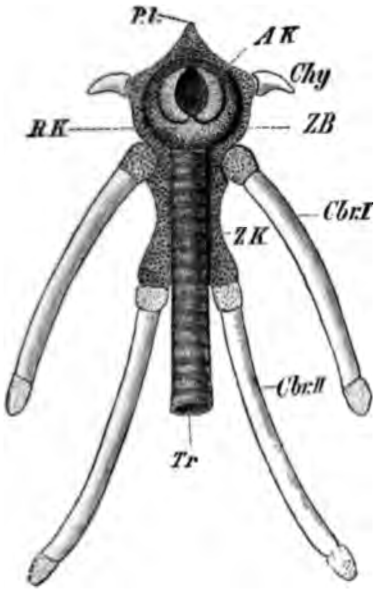

FIG. 85.—HYOBRANCHIAL APPARATUS, WITH LARYNX AND TRACHEA, OF *Emys europæa*. From the dorsal side.

AK, arytenoid cartilage of larynx; *Cbr.I*, *Cbr.II*, first and second branchial cornua; *Chy*, hyoid cornu; *P.l*, lingual process; *RK*, cricoid cartilage of larynx; *Tr*, trachea; *ZB*, broader anterior, and *ZK*, narrower posterior part of basihyobranchial.

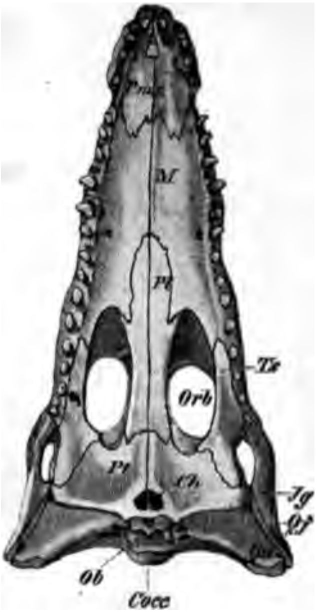

FIG. 86.—SKULL OF A YOUNG CROCODILE. Ventral view.

Ch, internal nostrils; *Cocc*, occipital condyles; *Jg*, jugal; *M*, palatine process of maxilla; *Ob*, basioccipital; *Orb*, orbit; *Pl*, palatine; *Pmx*, premaxilla; *Pt*, pterygoid; *Qj*, paraquadrate ("quadratojugal"); *Qu*, quadrate; *Ts*, transpalatine.

A series of air-passages extends into the bones from the tympanic cavity, and the Eustachian canals open into the pharynx by a median aperture behind the internal nostrils.

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[1] In the pre-Cretaceous Crocodiles the pterygoids did not form palatal plates.

The hyobranchial skeleton is much reduced, and consists of a body with a single pair of cornua: it is not known whether these belong to the hyoid or to the first branchial arch

Birds.

As already mentioned, the skull of Birds is formed on a similar plan to that of Reptiles—more particularly of Lizards, but it exhibits certain special characteristics (Figs. 87 and 88).

In correspondence with the higher type of brain, with its well developed cerebral hemispheres, the brain-case is relatively large, and correlative modifications occur, especially in the occipital and auditory regions. The relatively large size of the eyes, moreover, has resulted in a limitation of the cranial cavity in an anterior direction and in the expansion of the brain laterally and

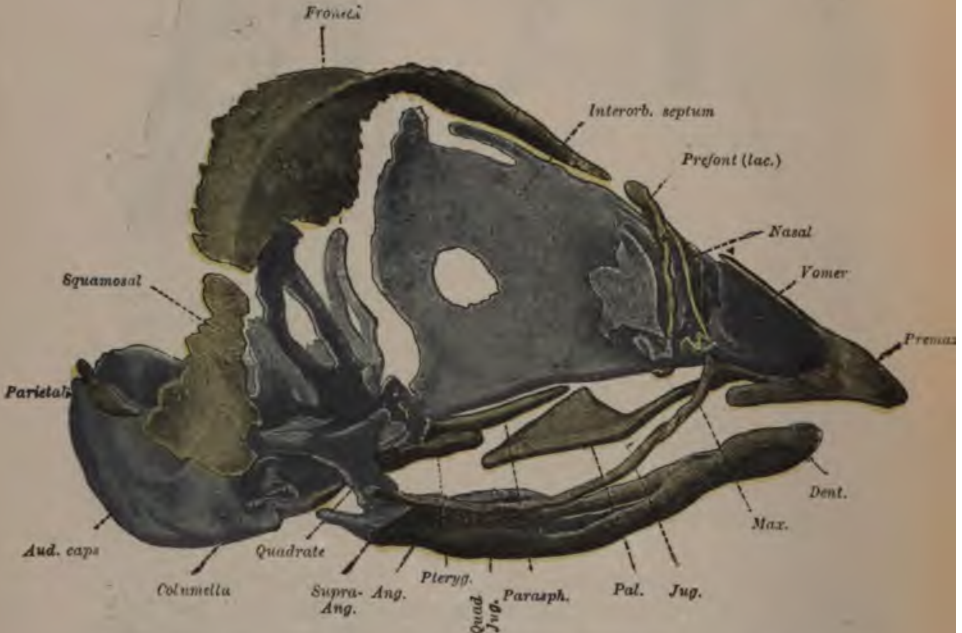

FIG. 87.—SKULL OF AN EMBRYO CHICK 65 MM. IN LENGTH. From the right side. (From a model by W. Tonkoff, × $\frac{4}{5}$). Cartilage, *blue*; investing bones, *yellow*.

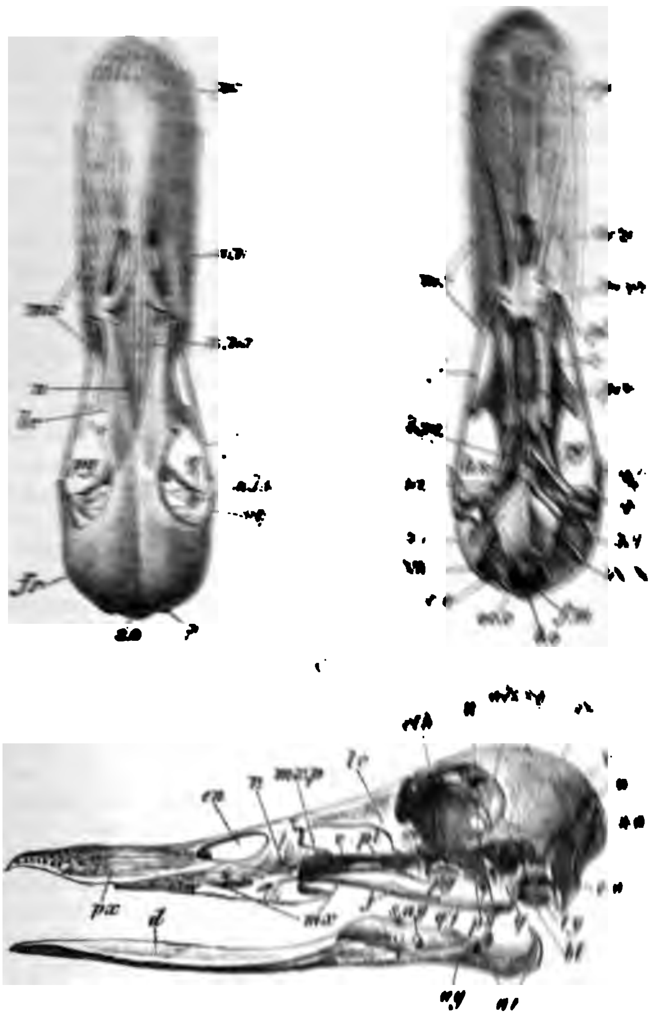

FIG. 88.—SKULL OF A WILD DUCK (*Anas boschas*). A, from above; B, from below; C, from the side. (From a preparation by W. K. Parker.)

ag, **angular**; *als*, **alisphenoid**; *a.p.f*, anterior palatine foramen; *ar*, articular; *b.o*, **basioccipital**; *b.pg*, **basipterygoid**; *b.s*, basisphenoid; *b.t*, basitemporal; *d*, **dentary**; *e.n*, external nostril; *e.o*, exoccipital; *eth*, ethmoid; *e.u*, **Eustachian aperture**; *f.m*, foramen magnum; *fr*, frontal; *i.c*, foramen for **internal** carotid artery; *j*, jugal; *lc*, lacrymal; *mx*, maxilla; *mx.p*, **maxillopalatine** process; *n*, nasal; *n.pr*, nasal process of the premaxilla; *p*, **parietal**; *pg*, pterygoid; *pl*, palatine; *p.n*, internal nostrils; *ps*, presphenoid; *px*, **premaxilla**; *q*, quadrate; *q.j*, quadrato-jugal; *s.o*, supraoccipital; *sq*, **squamosal**; *ty*, tympanic cavity; *v*, vomer; *II*, foramen for optic nerve; **V, for trigeminal**; *IX, X*, for glossopharyngeal and vagus; *XII*, for hypo**glossal**.

posteriorly. There is thus a well-developed interorbital septum. and the tropibasic type of skull reaches its extreme. The cranial cavity has become further enlarged at the cost of parts formerly situated extracranially than is the case amongst Reptiles. The bones show a tendency to run together by the obliteration of the sutures originally present between them; they are usually delicate and spongy ("pneumatic"), thus contrasting greatly with those of Reptiles.[1] Only in the ethmoidal region does the cartilage persist throughout life to any extent.

The unpaired occipital condyle no longer lies at the posterior boundary of the skull, but becomes relatively shifted forward along the base, so that the axis of the latter lies at an angle with that of the vertebral column.

The basis cranii is formed by a basioccipital and a basisphenoid, from which latter a bony rostrum, the remains of the anterior part of the parasphenoid, extends forwards: near the base of this, basipterygoid processes, articulating with the pterygoids, may be present. The posterior part of the parasphenoid persists as a large and primarily paired plate, the *basitemporal*, which underlies the basisphenoid and part of the basioccipital.

The interorbital septum is thin, as in Lizards, but is more solid and less membranous than in the latter: it becomes ossified anteriorly by a mesethmoid and posteriorly by a presphenoid. Orbitosphenoids and alisphenoids are also developed. The auditory capsules, which are more drawn in to the cranial cavity than in Reptiles, ossify by three centres (prootic, epiotic, and opisthotic) which later become fused with one another and with neighbouring bones, and the relations of the tympanic cavity, auditory fenestræ and columella, including the stapes and extracolumella, are very similar to those of Reptiles. The two Eustachian tubes open together in the middle line.

The quadrate is movable upon the skull as is also the whole maxillopalatine apparatus, the delicate palatopterygoid bar, which is always more or less separated from its fellow in the middle line, sliding on the rostrum of the basisphenoid, and so allowing the beak to be raised or lowered to a greater or less extent: thus a complete bony palate is never present. This mobility of the upper jaw is most marked in Parrots, in which the frontonasal joint forms a regular hinge.

The vomers, which may be absent, usually unite with one another and with the palatines to a greater or less degree.[2] The posterior nostrils are always situated between the vomers and palatines. The two premaxillæ, on the form of which depends that of the beak, are fused, and a maxillopalatine process arises from the maxilla anteriorly. The maxilla and quadrate are connected by a delicate jugal and quadratojugal, and a squamosal is present. Other investing bones are the nasals, frontals, parietals, and lacrymals or prefrontals.

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[1] It should, however, be remembered that the development of air spaces within the bones of the skull is hinted at in Crocodiles as well as in certain fossil Reptiles.

[2] The differences in details as regards the arrangement of the bones of the palate are important for purposes of classification, as are also the mode of connection of the lacrymal with surrounding parts, including the small bones (like those in Lizards) which may be present in the neighbourhood of the lacrymal (supraorbital, infraorbital, lacrymo-palatine).

Teeth were present in Jurassic and Cretaceous Birds (Archæopteryx, Hesperornis, Ichthyornis), but were no longer developed from the Tertiary period onwards, their place being taken functionally by horny sheaths covering the bones of the jaws, and thus forming a beak, much as in Chelonians.

In Meckel's cartilage, two replacing bones are formed, viz., an articular and a mentomandibular: the investing bones are a dentary, splenial, coronary, supra-angular, and an angular, and their relations are essentially similar to those seen in Reptiles: they, however, become fused in the adult, and the two rami of the mandible unite distally by synostosis.

The hyobranchial skeleton (Fig. 89) is greatly reduced. The median body consists of an entoglossal (basihyoid) passing anteriorly into a primarily paired paraglossal, which extends into the tongue, and posteriorly into a urohyal (basibranchial). The single pair of cornua belongs to the first branchial arch, and may, as in the Woodpecker, give rise to long, jointed rods extending far over the skull. The columella is the only part of the hyoid which persists, and even in the embryo there is no trace of a second branchial arch.

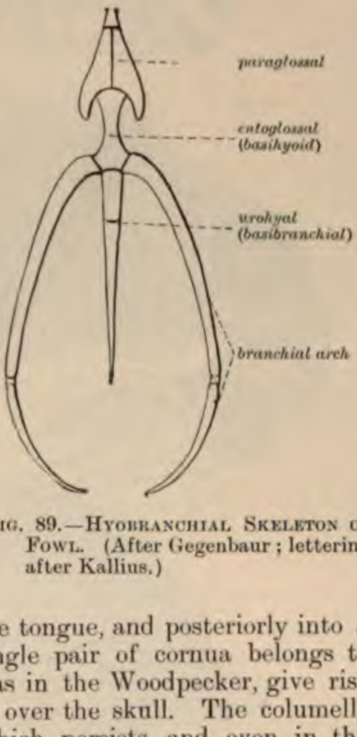

FIG. 89.—HYOBRANCHIAL SKELETON OF FOWL. (After Gegenbaur; lettering after Kallius.)

Mammals.

In Mammals, the skull of which in many respects indicates an origin of the Order from reptile-like ancestors, there is a much closer connection between the cranial and visceral regions than is the case in the Vertebrates already described. In the fully-developed skull both maxillary and palatopterygoid regions are closely united to the cranium, so that the facial and cranial portions are firmly united with one another. The higher we pass in the Mammalian series, the more does the former come to lie below instead of in front of the latter, the facial skeleton becoming proportionately small as contrasted with the large cranial portion

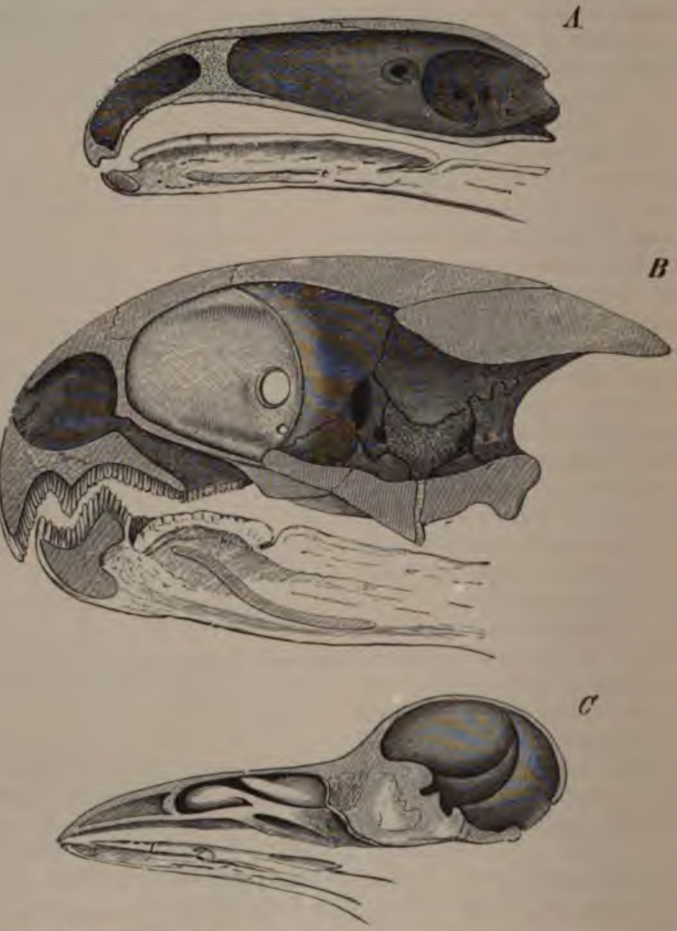

FIG. 90A.—LONGITUDINAL VERTICAL SECTIONS THROUGH THE SKULLS OF—A, *Salamandra maculosa*, B, *Testudo græca*, AND C, *Corvus corone*, TO SHOW THE RELATIONS BETWEEN THE CRANIAL AND NASAL PORTIONS.

of the skull, and the reduction of the angle between the basicranial and vertebral axes being carried still further than in Birds (cf. Fig. 90).

The base of the skull is mainly preformed in cartilage (Fig. 91), and is but little interrupted except for the passage of vessels and nerves. It consists of basioccipital, basisphenoidal and ethmoidal regions, continuous with one another and with the nasal septum. Side walls are also partly formed by the chondrocranium, but are

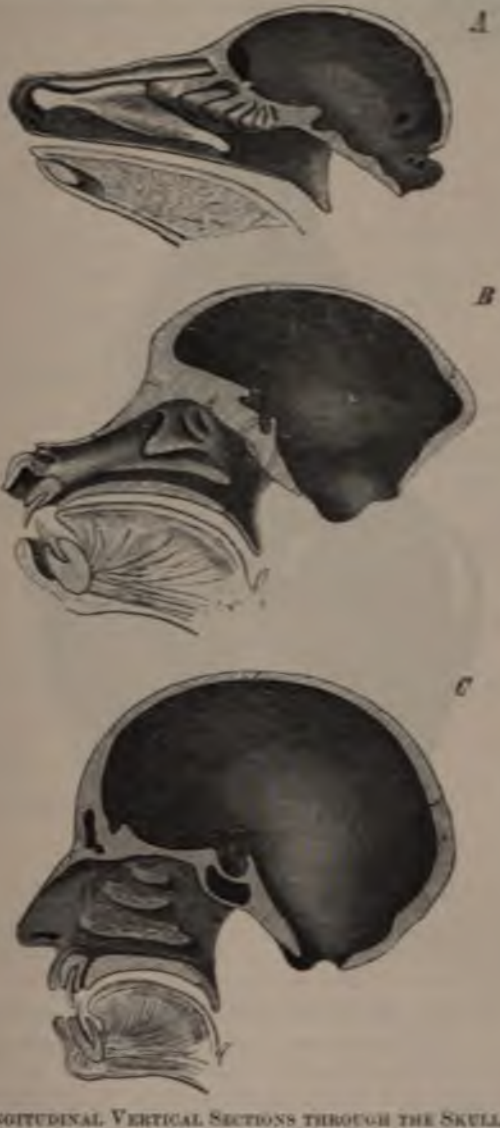

Fig. 90B.—Longitudinal Vertical Sections through the Skulls of A, Deer, B, Baboon, and C, Man, to show the Relations between the Cranial and Nasal Portions.

considerably fenestrated. The occipital region includes the equivalents of four vertebræ.

Apart from a median cartilaginous bridge connecting the anterior orbital region with the nasal capsules, and corresponding to the interorbital septum of the Sauropsida (by the ossification of which a presphenoid may arise), these capsules are connected

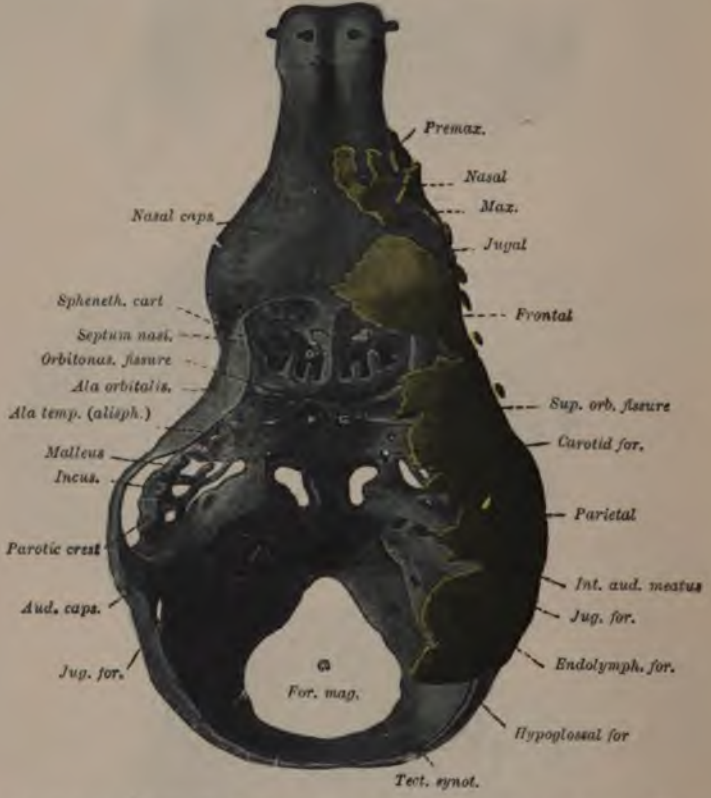

FIG. 91, A.—SKULL OF AN EMBRYO MOLE (42·3 MM. IN LENGTH FROM NOSE TO BASE OF TAIL). FROM AN ENLARGED MODEL, × $\frac{1}{3}$. A, dorsal, and B, ventral view. The investing bones are removed on the left side. (After E. Fischer.)

with the cerebral part of the chondrocranium merely by thin bars on either side (sphenethmoid cartilage): the Mammalian skull is therefore of the tropibasic type[1] (p. 77).

The anterior part of the basis cranii is formed by the ossification of the cartilage, which either gives rise to a distinct presphenoid, as already mentioned, or may be due to a union of the basal parts of the two orbitosphenoids. Alisphenoids, as well as a basisphenoid, a basioccipital, a supraoccipital, and exoccipitals (often with *paroccipital* or *paramastoid processes*) are always present, the paired condyle[1] being furnished by the exoccipitals (Fig. 92).

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[1] Certain facts in the development of the skull in Apes indicate that the Primates diverged very early from the common mammalian stem, many primitive characters being present which are no longer recognisable in other "lower" Mammals.

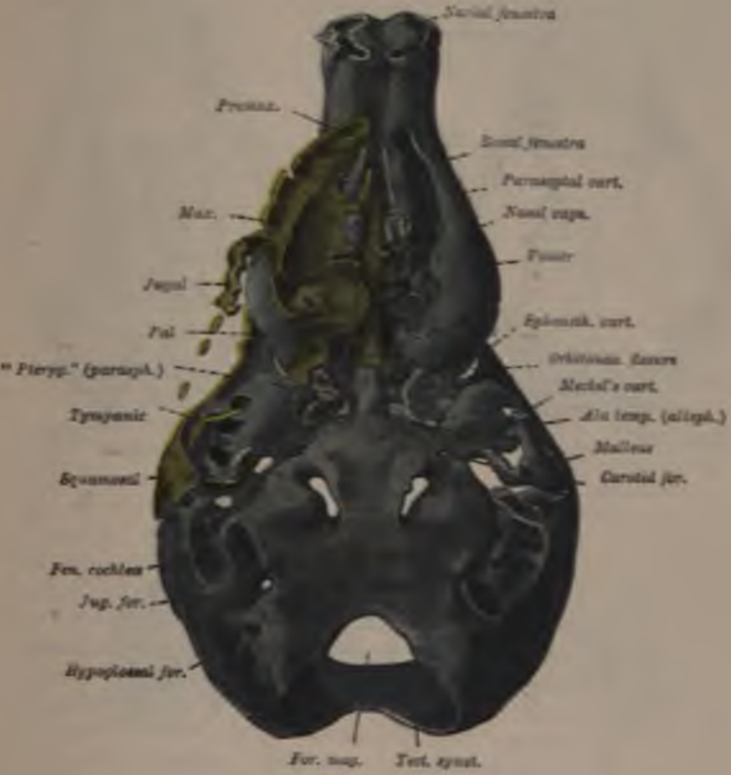

FIG. 91, B.

The enlargement of the cranial cavity in correspondence with the increased size of the brain affects the form of the skull in various respects. Thus the supraoccipital becomes shifted

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[1] The presence of two condyles appears at first sight to form an important difference to Reptiles, and this is the more remarkable as the occipital region has a similar primary constitution in both groups and differs from that of Amphibians. But in the case of the Sauropsida there are *four* points of connection between the occipital and the vertebral column. The single condyle is usually formed of three parts (p. 111), the median or axial of which articulates partly with the centrum proper of the atlas and partly with the odontoid process, with which it is connected by ligament. In Mammals, the lateral articulations are alone developed, and in the Mole embryo there is a single continuous articulation between the skull and vertebral column.

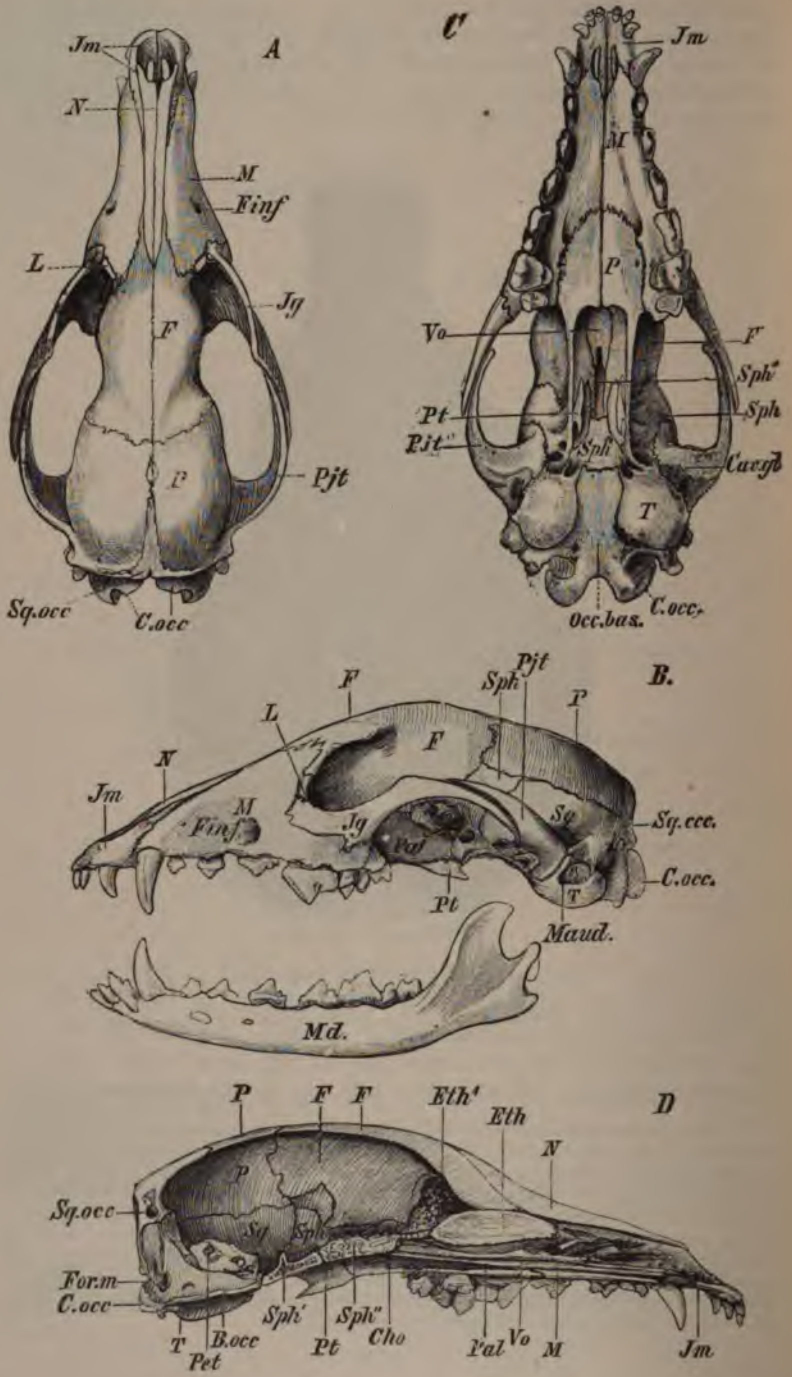
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FIG. 92.—SKULL OF GREYHOUND. A, from above; B, from the side; C, from below; and D, in longitudinal section.

B.occ, *Occ.bas*, basioccipital; *Cav.gl*, glenoid cavity for the lower jaw; *Cho*, posterior narial passage; *C.occ*, occipital condyles (exoccipitals); *Eth*, lamina perpendicularis of the ethmoid; *Eth'*, cribriform plate; *F*, frontal; *For.m*, foramen magnum; *Jg*, jugal; *Jm*, premaxilla; *L*, lacrymal, surrounding the lacrymal canal; *M*, maxilla, with the infraorbital foramen (*Finf*); *Maud*, external auditory meatus; *Md*, mandible; *N*, nasal; *P*, parietal; *Pal* (*P* in *C*), palatine; *Pet*, petrous portion of periotic; *Pjt*, zygomatic process of the squamosal; *Pt*, pterygoid; *Sph*, alisphenoid; Sph^1, basisphenoid; *Sph''*, presphenoid; *Sq*, squamosal; *Sq.occ*, supraoccipital; *T*, tympanic; *Vo*, vomer.

relatively backwards and the auditory region downwards to a varied extent, so that the squamosal (as is also the case in Birds) now usually helps to a greater or less extent to complete the walls of the brain-case dorsally to the displaced auditory capsule. Moreover, the course taken by the facial and auditory nerves through the skull-walls has become altered.[1]

In adaptation to the characteristic high development of the olfactory organs amongst Mammals, the ethmoidal portion of the skull is specially developed for enclosing the nasal cavities. The ethmoid is formed from the anterior part of the chondrocranium, which is continued forwards as the olfactory chamber, divided into right and left halves by a cartilaginous septum (mesethmoid), and separated from the cranial cavity by the cribriform plate (*lamina cribrosa*), which, however, is not directly homologous with that of lower types (p. 97): this has a more or less oblique or vertical position, according to the form and relations of the cerebral hemispheres and olfactory lobes. The posterior part of the mesethmoid becomes ossified as the *lamina perpendicularis*, and lateral ethmoids are present at the sides of the nasal region; the vomer, which is unpaired in the adult, arises as a paired perichondral bone ventrally to the nasal septum,[2] and the latter is thus in part bony.

The auditory capsules are ossified from prootic, epiotic, and opisthotic centres, which early unite together to form the *periotic* or *petromastoid* bone. The denser internal (petrous) portion of this bone, which corresponds mainly to the prootic, encloses the essential part of the organ of hearing, and a fenestra ovalis and fenestra rotunda are present on its outer surface: the more spongy mastoid

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[1] Considerable differences exist amongst Mammals as regards the number and arrangement of the nerve apertures. Thus amongst Carnivores, for example, the following foramina are distinct from one another: *opticum* (II), *foramen lacerum anterius* or *sphenoidal fissure* (III, IV, V^1, VI), *rotundum* (V^2), *ovale* (V^3), *meatus auditorius internus* (VII, VIII), *foramen lacerum posterius* (IX, X, XI), and the *condylar foramina* (XII). In the lower Mammals (*e.g.* Monotremes, Marsupials, and certain Insectivores), the optic foramen and sphenoidal fissure are not separate from one another, or, in some cases (Echidna, certain Insectivores, Dasypus, Lemurs), from the foramen rotundum. The cribriform plate of the ethmoid has numerous perforations for the olfactory nerve in all Mammals but Ornithorhynchus.

[2] In Ornithorhynchus a small dumb-bell shaped bone (*prevomer*) is present between the diverging premaxillæ.

(opisthotic) portion reaches the surface of the skull between the exoccipital and the *tympanic* bone, the homology of which is open to doubt, but which possibly corresponds to the paraquadrate or quadratojugal. The tympanic overlies the petrous portion of the periotic, and gives attachment to the tympanic membrane: in the Placentalia it forms the tubular external auditory passage or meatus below which it may expand into a *bulla tympani*, which encloses the tympanic cavity and communicates with the pharynx by means of the Eustachian tube. The "temporal bone" of human anatomy represents the fused periotic, tympanic, and squamosal, the two last of which are investing bones.

The cranial cavity is roofed in by frontals, parietals, and a supraoccipital: a primarily paired *interparietal*, not preformed in cartilage, may remain distinct or may unite with the supraoccipital or frontals. These roofing elements, like many of the other cranial bones, are united by sutures which usually persist, at any rate for a long time. Many of the bones are more or less spongy internally, and may contain definite air-sinuses (*e.g.* in Ungulates).

The parietals and frontals vary much as regards form and relative size in the different orders. In Primates, amongst many others, the parietals are well developed, while in Insectivores they are small: in toothed Whales they become separated from one another by a large bone formed by the fusion of the supraoccipital and interparietal, which reaches to the frontal (Fig. 94). In many Mammals there is a large parietal and supraoccipital crest in correlation with the strongly-developed muscles of the jaws and neck. The frontals, which, like many of the neighbouring bones, may become united together, extend downwards towards the orbital region and cribriform plate, and thus take part in forming the walls of the cranium and orbit.

Most of the true Ruminants are provided with *horns* or *antlers* projecting from the frontal bones, the formation of which is to be traced primarily to the integument (Fig. 93).

In the *Cavicornia* (Bovinæ, Antelopinæ, Caprinæ, Ovinæ) bony processes arise from the frontals, which become hollow and are enveloped by horn formed from the epiderm. They are usually present in both sexes, but in Tragelaphus, Neotragus, and others are absent in the female. In the *Cervidæ* a solid integumentary bone is developed and becomes united with the frontal, growing out to form the antler. After attaining its full development, the investing skin dries up owing to the development of the "burr" at its base; this constricts the vessels, and the antler, being deprived of nutriment, falls off periodically at the close of the breeding season. In the young animal the antlers are simple, but year by year they become more or less complicated and branched. They are confined to the male except in the case of the Reindeer. Amongst *Giraffes*, in addition to a short median "frontal horn" present in many of the sub-species, both sexes possess small lateral horns covered with hair: these are usually described as separate ossifications which become united with the frontals; but it has recently been shown that they originate in connection with the fibrous osteogenetic tissue of the parietal bones.

Dorsally and laterally to the cartilaginous olfactory capsules investing bones arise, viz., the variously-shaped nasals and the lacrymals, each of the latter perforated by a lacrymal foramen; in this region also are the lateral plates of the ethmoid (*laminæ papyraceæ*). The scroll-like *turbinals* which are usually well-developed within the olfactory chambers will be described later. Cartilage persists in the adult only in the nasal septum, in the form of the *alinasal* and *aliseptal cartilages*.[1] A septomaxillary

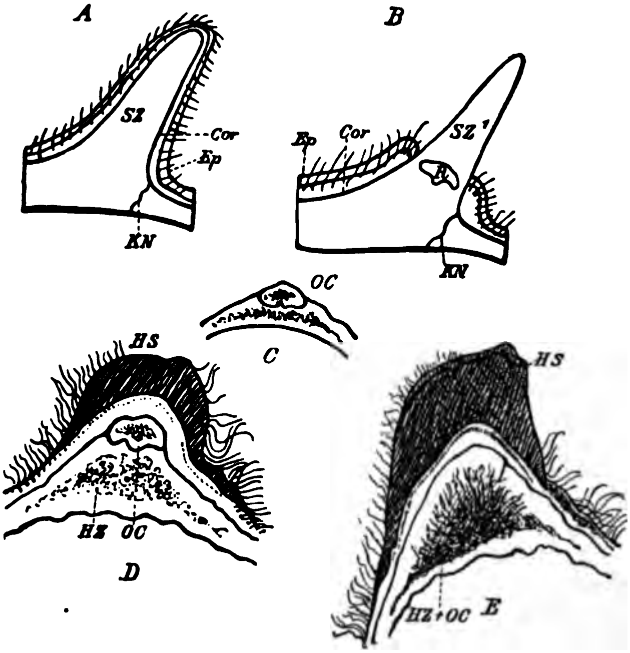

FIG. 93.—EARLY STAGES IN THE DEVELOPMENT OF ANTLERS (A, B) AND HORNS (C, D, E). (After M. Weber.)

Cor, derm; *Ep*, epiderm; *HS*, horny sheath; *HZ*, bony process of the frontal, with the epiphysis-like "os cornu" (*OC*) at its apex: the latter is comparable to the beam of the antler, and the former to the pedicle: in *E* the two are already fused (*HZ*+*OC*); *R*, zone of resorption, at which point the antler is shed; *SZ*, process of the frontal still covered with the integument; *SZ*¹, the same after loss of the integument.

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[1] An *external nose* is peculiar to certain Mammals (*e.g.* Man). Representatives of the cartilages mentioned above are present amongst other Amniota and in Reptiles, in which, however, they do not extend anteriorly to the rest of the

(cf. p. 82) can be recognised in embryos of Echidna close behind the external nostrils: it unites later with the premaxilla, forming its extra-nasal process, which in other Mammals possibly has a similar independent origin.

The premaxillæ, which may become fused, still take an important part in enclosing the nasal cavities, and in the Dugong (Halicore) they are very large and are bent downwards in correlation with the large pair of incisor tusks. The maxillæ form the larger part of the facial skeleton, and are also important in contributing to the walls of the nasal chambers and orbits. Each maxilla is connected by means of a jugal (malar) with a process of the squamosal, instead of with the quadrate, as in the Amphibia and Sauropsida; thus a zygomatic arch is formed from these three bones. The orbit and temporal fossa are marked off from one another in varying degrees: they are continuous, *e.g.* in Rodents, Insectivores, and Carnivores, while in Perissodactyles, Ruminants, and especially Primates, they are more or less completely separated from one another by a process of the frontal meeting the jugal.

As regards the structure of the hard palate, Mammals agree essentially with Crocodiles, and more or less complete palatine plates are formed by the premaxillæ, maxillæ, and palatines; but the small "pterygoids"[1] (except, *e.g.* in Anteaters and some Cetaceans) do not take part in its formation: in Echidna the pterygoids form part of the basis cranii. The palate is very long in Echidna and in certain Edentata and Cetacea, and often (*e.g.* Marsupialia) presents unossified vacuities.

The general form of the skull differs very greatly amongst Mammals. It is sometimes short and broad, sometimes elongated—especially in the region of the snout (*e.g.* Myrmecophaga, Cetacea). Amongst the Cetacea (Fig. 94), the facial bones are of so great a relative length that the skull may be one-third as long as the whole animal (*e.g.* Balæna); the external nostrils are situated far back, and there are numerous other secondary modifications apart from those seen in the lower jaw, which is not used for purposes of mastication and in certain respects shows traces of degeneration.

The genesis of the lower jaw is briefly as follows (Fig. 95). In the embryo, the proximal end of Meckel's cartilage is differentiated into two portions, corresponding to the articular and suspensorial

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skull, and are entirely covered by bones, the most important of which in this respect is the median nasal process of the premaxilla (Figs. 72, 80, 82, and 83). This prenasal process is present only in the Monotremes amongst Mammals, and with its fellow forms the transitory *os carunculæ*. On the loss of this ascending process of the premaxilla, a freer development of the cartilaginous skeleton is rendered possible; and under the influence of muscles, certain parts of it become separated off to form the independent cartilages of the external nose (cf. under Olfactory Organ).

[1] True pterygoid bones, corresponding to those of the Sauropsida, are apparently only known to occur in Monotremes. The so-called pterygoid (or internal lamina of the pterygoid process of the basisphenoid) of other Mammals *has been shown* to correspond to a posterior part of the parasphenoid.

parts of the jaw in the lower Vertebrates: these become ossified and enclosed within the tympanic cavity situated within the tympanic bone externally to the periotic. They thus represent

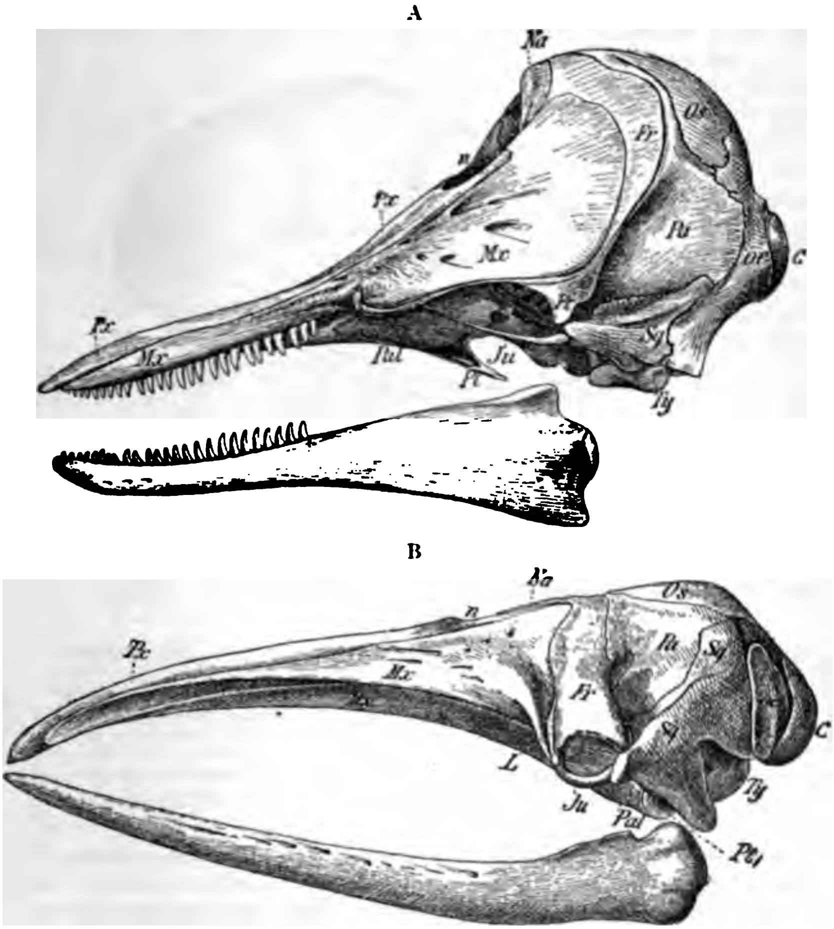

FIG. 94.—A, SKULL OF DELPHINUS. (From M. Weber, after Boas.) B, SKULL OF FOETAL *Balæna japonica*. (From M. Weber, after Eschricht.)

C, occipital condyle; *Fr*, frontal; *Ju*, jugal; *L*, lacrymal: *Mx*, maxilla; *n*, external nostril; *Na*, nasal; *oe*, exoccipital; *Os*, supraoccipital; *Pa*, parietal; *Pal*, palatine; *Pt*, pterygoid; *Px*, premaxilla; *Sq*, squamosal; *Ty*, tympanic and bulla tympani.

the articular and quadrate, and are known as the *malleus* and *incus* respectively. Having undergone a change of function, they form, together with a third element—the usually stirrup-shaped *stapes*, a connected and articulated chain of *auditory ossicles* extending between the fenestra ovalis and the tympanic membrane, and serving to conduct sound vibrations to the inner ear.[1] An investing bone, the dentary, is developed around the main part of Meckel's cartilage, distal to the malleus; the cartilage itself may undergo partial ossification, but gradually disappears, the dentary forming the bony mandible, which develops a new articulation with the squamosal, characteristic of, and confined to, the Mammalia, all other Craniata possessing the more primitive quadrato-mandibular articulation. The two rami of the lower jaw may remain distinct at the symphysis, or many unite with one another (*e.g.* Bats,

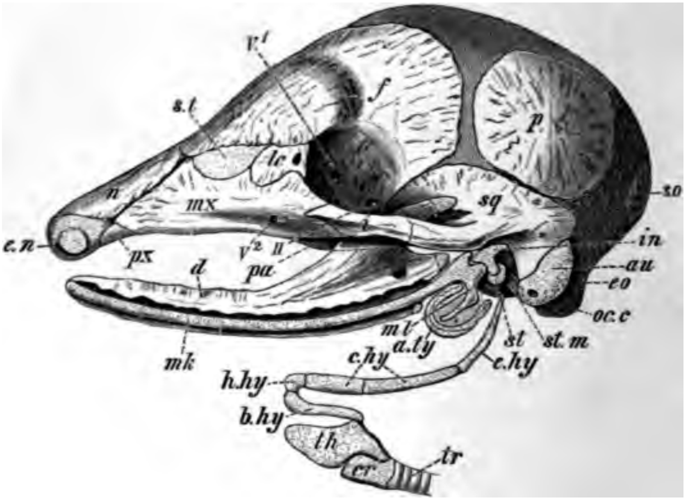

FIG. 95.—SKULL OF EMBRYO OF ARMADILLO (*Tatusia hybrida*). (Modified from a drawing by W. K. Parker.)

a.ty, tympanic annulus; *au*, auditory capsule; *b.hy*, basihyal; *c.hy*, ceratohyal; *cr*, cricoid; *d*, dentary; *e.hy*, epihyal; *e.n*, external nostril; *eo*, exoccipital: *f*, frontal; *h.hy*, hypohyal; *i*, jugal; *in*, incus; *lc*, lacrymal; *mk*, Meckel's cartilage; *ml*, malleus; *mx*, maxilla; *n*, nasal; *oc.c*, occipital condyle; *p*, parietal; *pa*, palatine; *px*, premaxilla; *so*, supraoccipital; *st*, stapes; *s.t*, ethmoturbinal; *st.m*, stapedius muscle; *sq*, squamosal; *th*, thyroid; *tr*, trachea; *II*, optic foramen; *V*¹, *V*², foramina through which the first and second divisions of the trigeminal pass out from the orbit.

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[1] There is some doubt as to how far it is justifiable to consider the tympano-eustachian cavity as homologous with the spiracle of Fishes, and the tympanic cavity and membrane of Amphibia, Sauropsida, and Mammalia as homologous with one another.

The stirrup form of the stapes is due to its being perforated by an artery (as in the case of the stapedial plate of the Gymnophiona), which in certain cases persists in the adult. The stapes, however, is not perforated in Monotremes and certain Marsupials and Edentates. The homology of this element is by no means clear, but there are reasons for considering it to correspond to the stapedial plate of the Sauropsida and to the whole columella of Amphibia; it is possible that all these structures are derivatives of the hyomandibular of *Fishes*.

Perissodactyles, Primates); and on each a condylar, a coronoid, and often an angular process (Marsupials, Rodents, Insectivores) may be distinguished.[1] Teeth, which are only exceptionally wanting (*e.g.* Echidna, certain Edentates), are confined to the premaxilla, maxilla, and mandible. They present marked differences in number, form, and size; together with the muscles, they are the cause of considerable modifications in the form of the jaws and their articulation and may indirectly influence the entire skull, in the study of which the law of correlation must always be borne in mind.

The hyoid arch (Fig. 95) is connected proximally with the base of the auditory capsule and sometimes becomes more or less ossified, but the greater part is usually reduced to a fibrous band, and may be quite rudimentary; its dorsal end forms the styloid process of the periotic, and its ventral end the lesser (anterior) cornu of the so-called hyoid bone of the adult. The body of this bone represents the basal parts of the hyoid and first branchial arch, the greater (posterior) cornua belonging to the latter. The hyoid apparatus is connected with the larynx by a membrane, the thyro-hyal ligament, and the thyroid cartilage of the larynx arises in the blastema of the second and third branchial arches.

V. APPENDICULAR SKELETON

The problem of the evolution and morphology of the fins and limbs of Vertebrates is one which, in point of interest and importance, is comparable to that relating to the head. During the last thirty years it has been attacked vigorously both from the embryological and the palæontological sides, and has given rise to so many speculations—often of a very contradictory nature—that only the barest outline of some of the more important results obtained can be given in the course of the present chapter.

The fins or limbs, which are distinguished from the *axial organs* (head, neck, and body) as *appendicular organs*, serve mainly for locomotion, and may be divided into two groups, the *unpaired* and the *paired* (pectoral and pelvic). They arise independently of the axial skeleton.[2]

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[1] Two or more small bones ("ossa mentalia") occur in Man between the distal ends of the mandibular rami, with which they unite, taking part in the formation of the mental prominence.

[2] Numerous and varied modifications of the fins occur amongst Fishes to form, *e.g.* organs for protection, support, attachment, offence, defence, or for alluring prey.

A. **Unpaired Fins.**

The unpaired, or median fins, which are mainly characteristic of Fishes, arise in the embryo as a ridge of the integument (ectoderm and mesoderm) extending along the median dorsal line from the anterior part of the trunk backwards to the tail, around the apex of which it is continued forwards for some distance along the ventral side: thus a dorsal, caudal, and ventral portion can be distinguished. In the course of further development, these portions either remain continuous, or else certain parts undergo reduction, so that the ridge only persists in certain regions, where it forms independent *dorsal*, *caudal*, and *ventral* or *anal fins* (Fig. 96, A, B): in these regions muscles and skeletal parts become developed in Fishes.

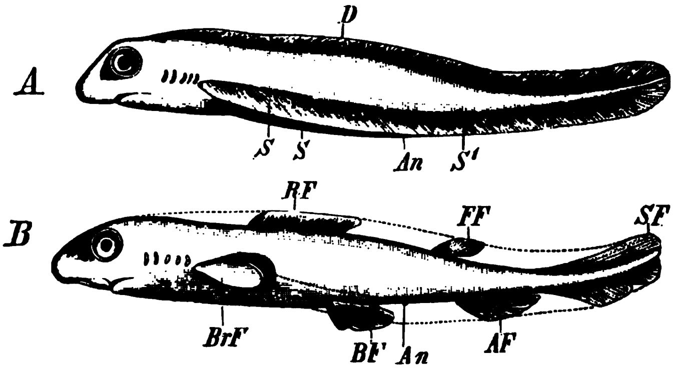

Fig. 96.—Diagram showing (A) the Undifferentiated Condition of the Paired and Unpaired Fins in the Embryo, and (B) the Manner in which the Permanent Fins are formed from the Continuous Folds.

AF, anal fin; *An*, anus; *BF*, pelvic fin; *BrF*, pectoral fin; *D*, dorsal fin-fold; *RF*, *FF*, dorsal fins; *SF*, tail-fin; *S*, *S*, lateral folds, which unite together at S^1 to form the ventral fold.

These skeletal parts consist of supporting rays of two kinds. In the base of the fin *cartilaginous radii*, or *pterygiophores*, usually segmented (typically into three portions), are formed; these may unite proximally to form one or more *basipterygia*, and in bony Fishes they become extensively ossified: they frequently come into secondary connection with the vertebral column. Except in Cyclostomes, the peripheral part of the fin is supported by *dermal rays*, which may consist of numerous delicate *horny* fibres (Elasmobranchs), or of *bony* rods, entire or jointed, often cleft at the base, and articulating with the pterygiophores, and not preformed in cartilage (Teleostomes): recent researches indicate that the latter are ectodermal in origin.[1]

Median fins are also present in the Amphibia, in which they may persist throughout life (*e.g.* Perennibranchiata), or only occur in the larval stage; occasionally also they become specially developed during the breeding season (*e.g.* Newt). They have the form of a continuous integumentary fold extending round the tail and along the back for a greater or less distance, but enclose no skeletal elements.

Amongst Reptiles one or more median fins were present in Ichthyosaurus, and these are comparable to the dorsal fins occurring in the Cetacea amongst Mammals: in both cases they, like the *horizontal* tail fin of these forms, must be looked upon as structures acquired secondarily in connection with an aquatic existence.

B. Paired Fins or Limbs.

As regards the origin of the paired fins, there is much difference of opinion. According to one view, they correspond to modified gill-arches and rays, the former giving rise to the pectoral and pelvic arches or girdles, and the latter to the free portion of each fin, one of the rays becoming enlarged so that the others are attached in a row on either side of it, instead of to the arch. This would result in a biserial form of fin, the "*archipterygium*" of Gegenbaur, such as is most nearly retained in Ceratodus (Fig. 118), and is also indicated in many Elasmobranchs. The fact that the branchial arches are situated in the pharyngeal wall and the limb arches in the body-wall, alone forms an important objection to this theory.

Another view, which seems to be the more likely one, is as follows. It is highly probable that primitive Vertebrates at one time possessed, in addition to the median fins, a pair of continuous *lateral fin-folds*, traces of which, beginning with a proliferation of the mesoderm, can still be recognised in young embryos of Elasmobranchs (Fig. 97) and to a less extent in those of other Fishes and of Amphibians, and which, though never continuous, are indicated by muscle-buds on the intermediate myotomes. They extended backwards along the sides of the body from just behind the head, gradually converging towards the anal region, where they became continuous with the ventral part of the median fin-fold (Fig. 96, A), and in this respect resembled the persistent *lateral* or *metapleural folds* present in the adult **Amphioxus,** though it is doubtful how far this comparison is justifiable. As is usually the case in the median fins, certain parts of these lateral folds have undergone reduction, only the anterior and posterior portions remaining to form respectively the pectoral and pelvic fins, which must therefore be looked upon as the localised remains of a continuous lateral fin-fold on either side of the body.[1]

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[1] The dermal fin rays or *dermotrichia* are classified by Goodrich as follows:— 1. Horny *ceratotrichia* in Elasmobranchs; 2. Bony *leptotrichia* in Teleostomes; 3. Horny *actinotrichia* occurring in the embryo and in the margins of the fins of adult Teleostomes, in addition to (2); 4. Fibrous, calcified, or horny *camptotrichia* in Dipnoans: it is doubtful whether the last-mentioned correspond to (1) or to (2).

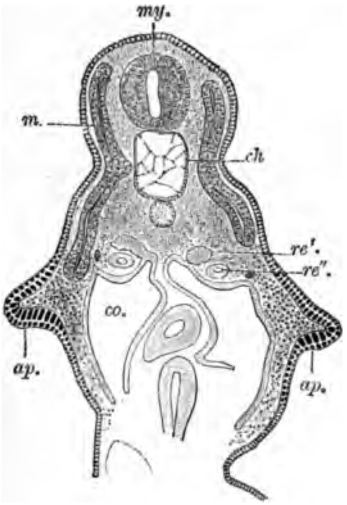

Fig. 97.—Transverse Section through the Embryo of a Shark (*Pristiurus melanostomus*), 9 mm. long, showing the Mode of Origin of the Pectoral Limb-Buds.

ap, limb-buds; *ch*, notochord; *co*, cœlome; *m*, myomeres, which are extending ventrally; *my*, spinal cord; *re'*, *re"*, rudiment of kidney tubule and duct.

Into these paired folds extend metameric processes of the myomeres, which undergo further development in those regions which will give rise to the pectoral and pelvic fins, and disappear in the intermediate region. More or fewer spinal nerves pass into the fins, and finally also cartilaginous supports (pterygiophores), as in the case of the median fins. These radii appear first of all at the base of the fin, gradually extending centrifugally into the latter, and also, becoming fused, centripetally into the body-wall (Fig. 98).[2] An articulation is then formed secondarily between the fused basal part of the skeleton situated in the free portion of the fin (*basipterygium*) and that which extends into the lateral body-wall and serves as a support for the limb proper: this constitutes the *limb-arch* or *girdle*.

The arch may remain comparatively small and not extend far dorsally; but when the extremity is destined to perform more important movements in locomotion or to give a more definite support to the body, in addition to meeting with its fellow ventrally, the arch may extend upwards so as to come into connection with the axial skeleton, thus forming an almost complete girdle around the body. The parts of the limb-skeleton may become ossified later. The pelvic fin of Fishes as a rule remains at a simpler and more embryonic stage than the pectoral fin.

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[1] The essential part of this conception as to the origin of the paired extremities is due to Thacher, Mivart, Balfour, Haswell, and Dohrn, and a somewhat similar idea was put forward by Goodsir as early as 1856. The Palæozoic Cladoselache is very suggestive in this respect.

[2] Thus phylogenetically both anterior and posterior extremities can be traced to a metameric ground-plan. At the same time it must be borne in mind that the above account is not altogether borne out ontogenetically. The muscle-buds are not strictly metameric, as they fuse together before coming into connection with the skeletal parts, with which they do not always correspond numerically and which appear to consist at first of a single unsegmented basipterygium: in other words, the radii arise secondarily. Moreover, it is held by some embryologists that ontogenetically the girdle is the primary part of the extremity from which the free portion grows out secondarily, and a similar axifugal growth can be recognised in the median fins. All this, however, may only mean that *recapitulation is incomplete*, and the arguments against the lateral fin-theory are still not *conclusive*.

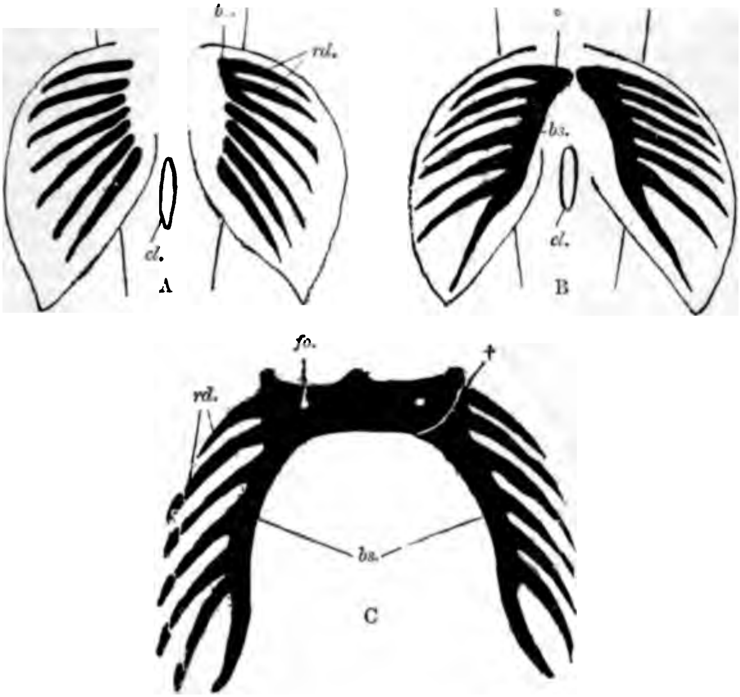

Fig. 98.—A, B, C. Diagram of Three Successive Stages in the Development of the Pelvic Fin of a Shark.

cl, **cloacal aperture**; *fo*, obturator foramen; *rd*, primitive radii, which in A are beginning to fuse into a basal plate (*bs*). In B this fusion has taken place on both sides, and at * the proximal ends of the two basals are approximating to form the arch. In C the process is completed, and at † an articulation has been formed between the arch and the free portion of the fin. On the left side in C the radii are becoming secondarily segmented.

The paired extremities are not connected with any particular body-segments, but vary greatly as to their relative positions and the nerves which supply them.

Pectoral Arch.

Fishes.—Paired fins and arches are wanting in Cyclostomes. In Elasmobranchs the pectoral arch consists of a comparatively simple cartilaginous bar (Fig. 99), situated just behind the branchial apparatus, the two halves of which are united ventrally by cartilage or fibrous tissue,[1] and in embryos of Teleostomes it has at first a similar structure. Later, however, in the last-named Order, bony structures originating from the integument are developed in this region; so that a *secondary* or bony pectoral arch may be distinguished from a *primary* or cartilaginous one, the latter becoming less marked in proportion to the development of the former (Fig. 100).

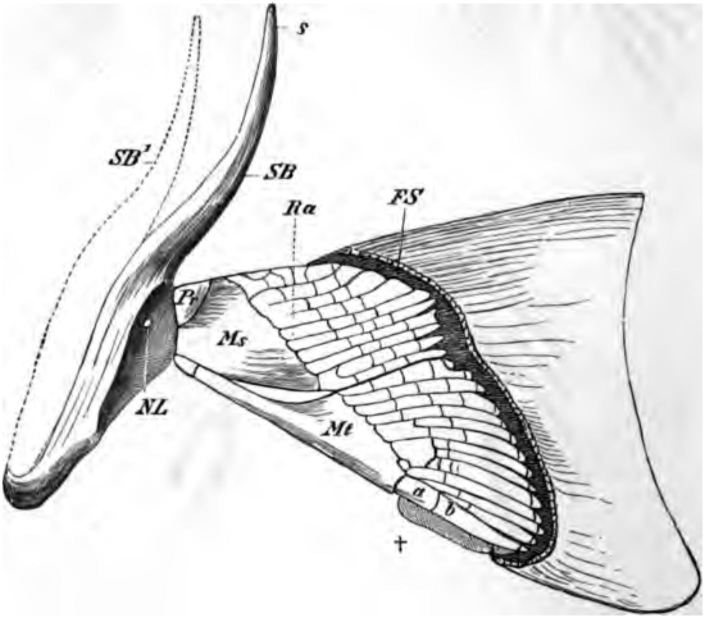

Fig. 99.—Pectoral Arch and Fin of *Heptanchus*.

a, *b*, the main fin-ray, lying in the axis of the metapterygium (*Mt*); †, single ray on the other side of the axis (indication of a biserial type); *FS*, horny rays, cut through; *Pr*, *Ms*, *Mt*, the three basal elements of the fin (pro-, meso-, and metapterygium); *Ra*, fin-rays; *SB*, *SB*^{1}, pectoral arch, with a nerve aperture at *NL*.

In all Fishes the free extremity, or fin, is connected with the hinder and outer circumference of the (primary) arch, convex articulations being formed on the arch which fit into concave facets on the fin. The point of attachment of the extremity may be taken as separating the arch into an upper dorsal and a lower ventral section. The former, which may exceptionally be connected with the vertebral column (viz., Raiidæ), corresponds to the *scapula*, and the latter to the *coracoid* plus *procoracoid* of the higher Vertebrata.

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[1] In Heptanchus there is a small ventral element which has been compared to a "sternum."

In Teleosts and bony Ganoids the secondary arch, consisting of a row of bones, forms the principal support of the fin in the adult, the main element being a large *clavicle*. The arch becomes secondarily connected with the skull. (For further details, cf. Fig. 100.) In Dipnoans, clavicles and supra-clavicles invest the cartilaginous arch (Fig. 71).

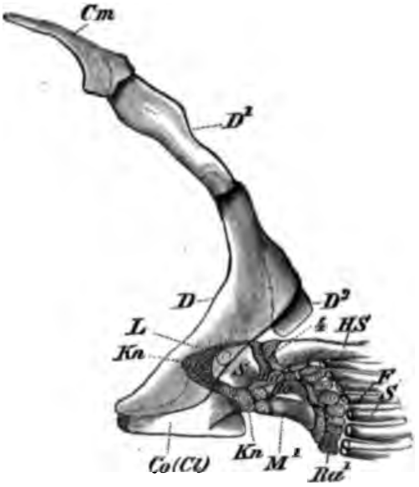

FIG. 100.—LEFT PECTORAL ARCH AND FIN OF THE TROUT. (From the outer side.)

D, D^1, D^2, chain of secondary bones of the pectoral arch (clavicle and supraclavicle), which is connected with the skull by means of the post-temporal (*Cm*); *F*, *S*, bony fin-rays, shown cut away from their attachments; *HS*, bony ray on the border of the fin which is connected with the fourth basal element; *L*, foramen in scapula; M^1, metapterygium; *Ra*, *Ra*, the second and third, and 4, the fourth basal element of the fin; Ra^1, the second cartilaginous row of radii; *S* and *Co*(*Cl*), bony scapula and coracoid, which have become developed in the cartilage *Kn*.

Amphibians.—In this Class the pectoral arch shows no direct connection with that of Fishes, but is similar in fundamental plan to that of all the higher Vertebrates.

It always consists on either side of a cartilaginous or bony dorsal plate (*scapula* and *suprascapula*), which curves round the side of the body and is continuous with two ventral plates—an anterior (*procoracoid*) and a posterior (*coracoid*) (Figs. 101 and 102). The ventral part of the arch becomes connected with the sternal apparatus. The humerus articulates with a concave glenoid facet at the junction of the scapula and coracoid. The two coracoid plates either overlap one another in the mid-ventral line (Urodeles, Fig. 55, A, B and certain Anura—*e.g.* Hyla, Bombinator, Fig. 55, C), or else their free edges come into apposition and unite (other Anura, *e.g.* Rana, Fig. 55, D). In Anurans the procoracoid has a more transverse position than in Urodeles, and comes into connection with the coracoid in the mid-ventral line, thus giving rise to a fenestra between the two.

The whole arch is, moreover, more strongly ossified, the procoracoid being covered by an investing bone—the *clavicle*, which may more or less completely replace it. This integumentary bone corresponds to the part of the secondary arch which first appears in Ganoids: in the Stegocephali there was a well-developed clavicle connected with the episternum (see p. 44) and peripherally with another bony rod (cleithrum), which also occurred in the fossil Reptile Pareiasaurus.

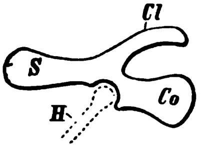

FIG. 101.—DIAGRAM OF THE GROUND-TYPE OF PECTORAL ARCH MET WITH IN ALL VERTEBRATA FROM AMPHIBIA TO MAMMALIA.

Cl, procoracoid; *Co*, coracoid; *H*, humerus; *S*, scapula.

Reptiles.—As in Amphibians, the most essential parts of the pectoral arch of Reptiles are the scapula and coracoid, arising in connection with a continuous cartilaginous bar or plate, as is well seen in Lizards (Fig. 56). A procoracoid may also be formed, and in Chelonians a bone usually described as the procoracoid is strongly developed, but is firmly united with the pillar-like scapula, the two being separated from the coracoid by a suture; hence the bone in question is sometimes spoken of as a *proscapula*. In other recent Reptiles the procoracoid is much reduced or even absent.

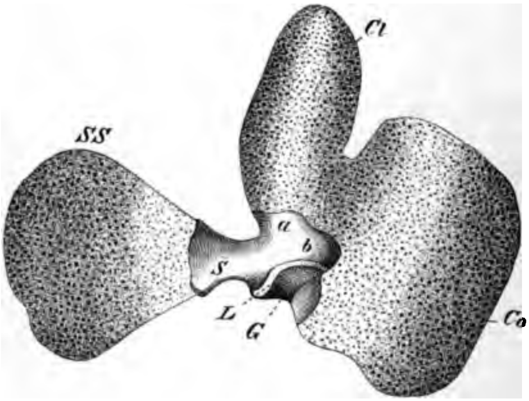

FIG. 102.—PECTORAL ARCH OF THE RIGHT SIDE OF *Salamandra maculosa*, considerably magnified, and flattened out.

a, *b*, bony processes extending into the procoracoid and coracoid respectively; *Cl*, procoracoid; *Co*, coracoid; *G*, glenoid cavity, surrounded by a rim of cartilage (*L*); *S*, scapula (ossified); *SS*, suprascapula.

Traces of the relations of the procoracoid to the clavicle can still be seen in some cases, but the latter, when present, arises mainly from a connective-tissue blastema unconnected with a procoracoid (Fig. 56). Nevertheless a primary and a secondary part of the pectoral arch can also be recognised in Reptiles, the former represented by the more constant elements, while the latter tends to become reduced and may even entirely disappear. Clavicles are absent in Chelonians, and are either wanting or rudimentary in Crocodiles and Chameleons.

On the loss of the extremities (certain Skinks, Amphisbænians, Snakes), the primary shoulder-girdle becomes reduced or even entirely lost, the reduction beginning with the sternum.

The shifting backwards of the pectoral arch, which is already to some extent seen in Amphibians as compared with Fishes, is still more marked in Reptiles, in which it is situated some distance from the head; this is especially seen in Chelonians and many fossil forms, and reaches its maximum in Birds.

In Lizards, unossified spaces are left in the coracoid, giving rise to fenestræ closed over by fibrous membrane. A main fenestra (cf. Fig. 56, *a*, dorsal to which a bony process, the vestigial procoracoid, can be seen) may be distinguished from accessory fenestræ of varied form and number, and is typical of all Lizards: it arises in the primary arch and corresponds to that occurring in Amphibians (Fig. 55).

Birds.—In Birds, the scapula consists of a thin and narrow plate of bone often extending far backwards, the strong coracoid being bent at an acute angle and united by ligament with it in typical Carinate Birds (Fig. 53). In the Ratitæ the relatively small scapula and coracoid are ankylosed with one another. The lower end of the latter bone is firmly articulated in a groove on the anterior edge of the sternum, while its upper end takes part with the scapula in forming the glenoid cavity, beyond which it is produced in the Carinatæ and in Archeopteryx to form an *acrocoracoid process*.

In Struthio the broad coracoid is fenestrated, and its anterior part may be looked upon as a procoracoid: in other Ratitæ the latter is considerably reduced, and may be represented merely by a ligament; in Carinatæ it can often no longer be recognised.

In almost all Flying Birds the clavicle, a purely dermal bone, is well developed, and becomes united with its fellow to form a *furcula* (Fig. 53). Amongst the Cursorial Birds, the Emu and Cassowary possess vestigial clavicles: in the others they are wanting, and they have also undergone more or less complete reduction in some Carinate Birds (*e.g.* certain Parrakeets and Owls).

Mammals.—In Monotremes the pectoral arch retains primitive characters, and in them only amongst Mammals does the coracoid extend ventrally to reach the sternum (Fig. 103); in all other members of this Class it characteristically becomes reduced,[1] and simply forms a prominent process on the scapula (*coracoid*

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[1] In early stages of certain Marsupials (*e.g.* Trichosaurus), and possibly in all, the coracoid is well developed and articulates with the sternum, but it subsequently undergoes reduction.

process), which is ossified from a separate centre, apparently representing an epicoracoid, while the coracoid proper may be occasionally indicated by a small centre of ossification on the glenoid margin of the scapula.

Thus the scapula becomes freer from the rest of the skeleton, and it alone serves to support the extremity; it becomes at the same time greatly broadened, and gives rise on its outer side, in connection with the highly differentiated muscles of the limb, to a strong ridge (spina scapulæ), which extends downwards to form the so-called acromion. The distal end of the clavicle usually becomes connected with the acromion, its proximal end articulating with the anterior edge of the sternum.

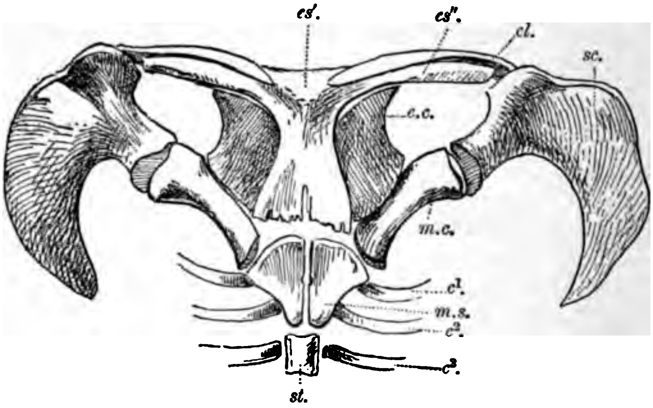

FIG. 103.—PECTORAL ARCH AND STERNUM OF *Ornithorhynchus paradoxus*.

c^1, c^2, c^3, first, second, and third ribs; *cl*, clavicle; *e.c*, epicoracoid; *es*^{1} and *es*^{2}, prosternum (episternum); *m.c*, coracoid (metacoracoid); *m.s*, manubrium sterni; *sc*, scapula; *st*, sternebra.

In those Mammals in which the fore-limbs are capable of very varied and free movements (Lemurs, certain Marsupials, many Rodents and Insectivores, Bats, and Primates) the clavicles are strongly developed.[1] In others (*e.g.* Ungulates, Cetaceans, Carnivores, most Edentates, Rodents, Marsupials) they may be entirely wanting or only vestigial, and in the latter case their relations to the scapula become altered.

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[1] The clavicle is primarily independent of the coraco-scapular portion of the pectoral arch. Its original dermal character is retained in Monotremes, but in all other Mammals it is developed on a cartilaginous basis.

Pelvic Arch.

Fishes.—In Cartilaginous Ganoids, indications of a pelvis are seen, but are very variable, even in individuals of the same species. They consist of two calcified or ossified *pelvic plates*, which correspond to portions segmented off from the basal cartilage (basipterygium) of the fin. In some cases even this segmentation does not take place, and thus the pelvis remains undifferentiated. This simple condition is also met with in the ancient forms Pleuracanthus and Xenacanthus (Fig. 104, A, B).

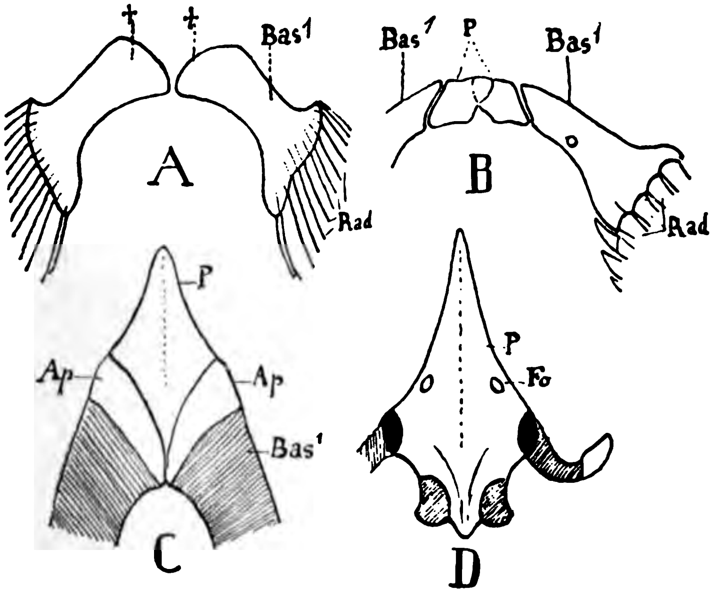


FIG. 104.—SIMPLE FORMS OF PELVIS AMONGST FISHES AND AMPHIBIANS.

A, *Pleuracanthus*—the pelvis is here not differentiated from the proximal end (††) of the basipterygium; B, *Scaphirhynchus cataphractus*; C, *Polypterus bichir*; D, *Necturus* (*Menobranchus*). *Ap*, apophysis of the basipterygium; *Bas¹*, basipterygium; *Fo*, obturator foramen; *P*, pelvis; *Rad*, radii.

In Polypterus the pelvis shows some advance on that of Sturgeons. Owing, doubtless, to the necessity of a firmer connection of the fin with the body-wall, the two pelvic plates become united together in the mid-ventral line (Fig. 104, C). In spite, however, of the rudimentary character of the pelvis of Polypterus, the essential form of that of the Dipnoi and Amphibia (D) is already sketched out (for Teleosts, cf. p. 159).

The pelvis of Elasmobranchs consists of a tranverse bar extending between the two basipterygia, from which it has become segmented off secondarily (Fig. 98): it is perforated by nerves, and gives rise on either side to an iliac process (most marked in the Holocephali) extending upwards into the lateral walls of the body (Fig. 105). A *prepubic process* is also present, and there is apparently also an indication of a median epipubic process (cf. *infra*). The whole pelvic plate essentially corresponds, more or less completely, with the *ischiopubis* of higher forms.

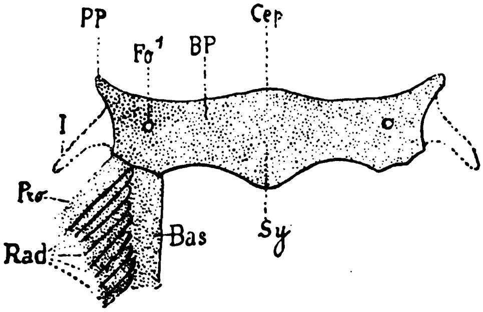


FIG. 105.—DIAGRAM OF THE ELASMOBRANCH PELVIS. From the ventral side.

Bas, *Pro*, *Rad*, basipterygium, propterygium, and radii of the fin; *BP*, pelvic plate (ischiopubis); *Cep*, epipubic process; *Fo*^{1}, obturator foramen; *I*, iliac process; *PP*, prepubic process; *Sy*, region of the ischiopubic symphysis.

In the Dipnoi, the narrow cartilaginous pelvic plate (Fig. 106) is provided with a long and delicate anterior median, a short posterior median process, and two pairs of lateral processes. Of the latter the anterior (prepubic processes) are much longer in Protopterus than in Ceratodus, and each is embedded in an intermuscular septum; with the posterior process the skeleton of the fin is articulated by means of an intermediate piece. The anterior unpaired process may be looked upon as an *epipubic process*, corresponding with that of Amphibia and Amniota (*q. v.*). The posterior or hypoischiatic process bears a ridge for the attachment of muscles.

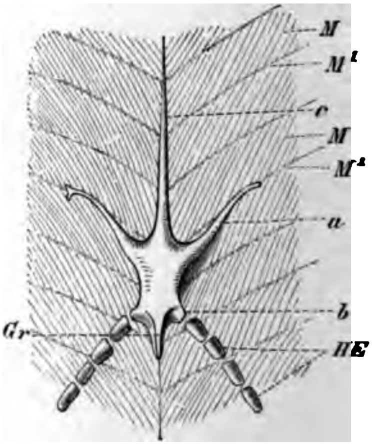
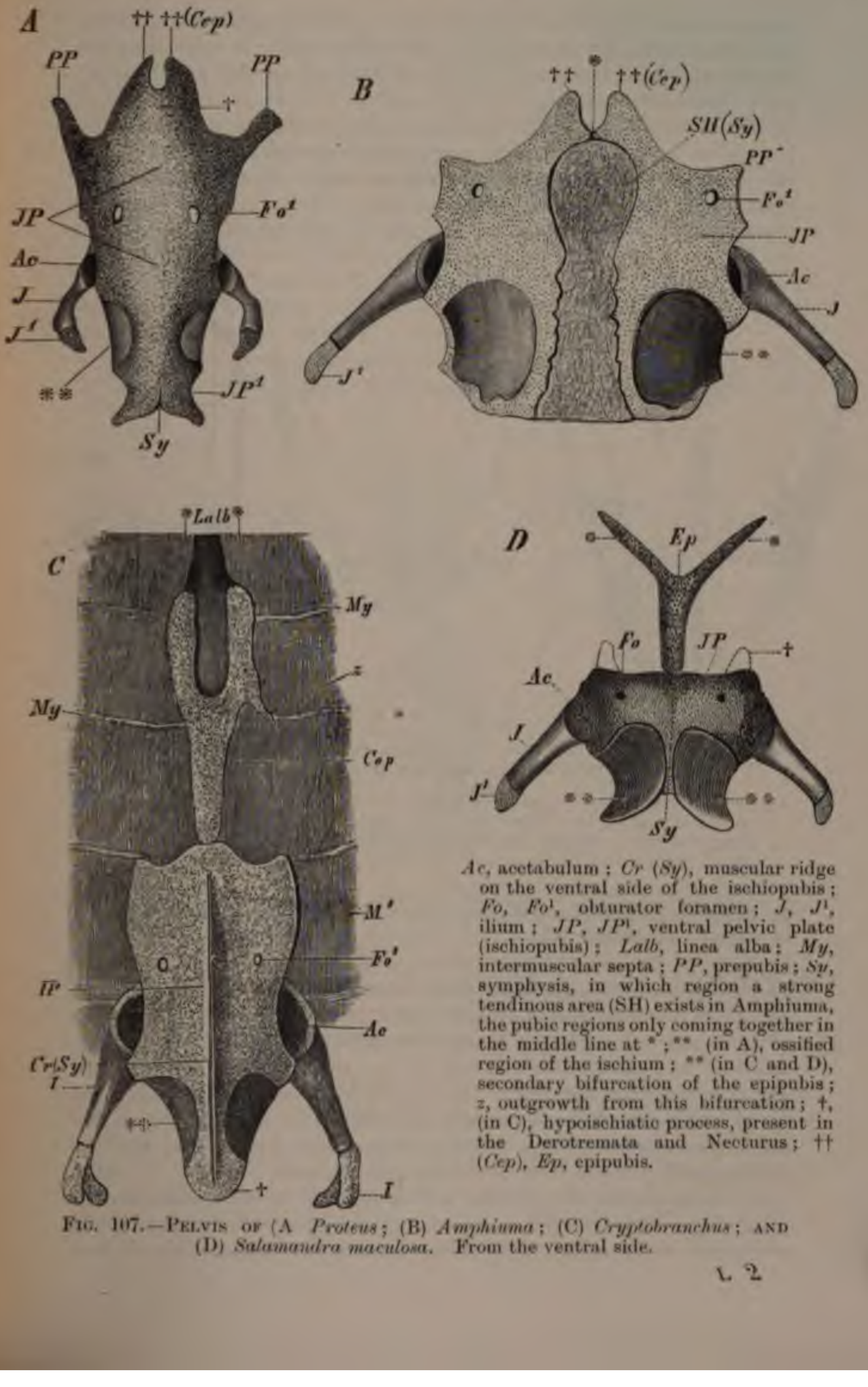


FIG. 106.—PELVIS OF *Protopterus*. From the ventral side.

a, prepubic process, which may become forked at its distal end; *b*, process to which the pelvic fin (*HE*) is attached; *c*, epipubic process; *Gr*, ridge for attachment of muscles; *M*, myotomes; *M*^{1}, intermuscular septa.

Amphibians.—It will be seen by a glance at Fig. 104, D, that the ventral portion of the pelvic arch of Necturus is formed on the same plan as the pelvic plate of the Dipnoi and Crossopterygii, but in all Urodela and Amniota it is perforated by the obturator nerve. Like the pelvis of all Vertebrates, it has a paired origin, and in **Proteus and**



Ac, acetabulum ; *Cr* (*Sy*), muscular ridge on the ventral side of the ischiopubis ; *Fo*, *Fo*^{1}, obturator foramen ; *J*, *J*^{1}, ilium ; *JP*, *JP*^{1}, ventral pelvic plate (ischiopubis) ; *Lalb*, linea alba ; *My*, intermuscular septa ; *PP*, prepubis ; *Sy*, symphysis, in which region a strong tendinous area (SH) exists in Amphiuma, the pubic regions only coming together in the middle line at * ; ** (in A), ossified region of the ischium ; ** (in C and D), secondary bifurcation of the epipubis ; z, outgrowth from this bifurcation ; †, (in C), hypoischiatic process, present in the Derotremata and Necturus ; †† (*Cep*), *Ep*, epipubis.

FIG. 107.—PELVIS OF (A *Proteus* ; (B) *Amphiuma* ; (C) *Cryptobranchus* ; AND (D) *Salamandra maculosa*. From the ventral side.

Amphiuma this is indicated by the fact that its anterior epipubic process is paired throughout life (Fig. 107, A, B). In the Derotrema and Myctodera, the anterior end of the median epipubic process is bifurcated (C, D).

As already indicated, the ischiopubic plate is phylogenetically the oldest part of the pelvis, and various modifications as regards the degree of its fusion into a median unpaired plate and of its ossification occur amongst Amphibians; the typical triradiate arrangement of the pelvic bones (*ilium*, *ischium*, and *pubis*), such as is further differentiated in certain Stegocephali and in Reptiles, is already sketched out.

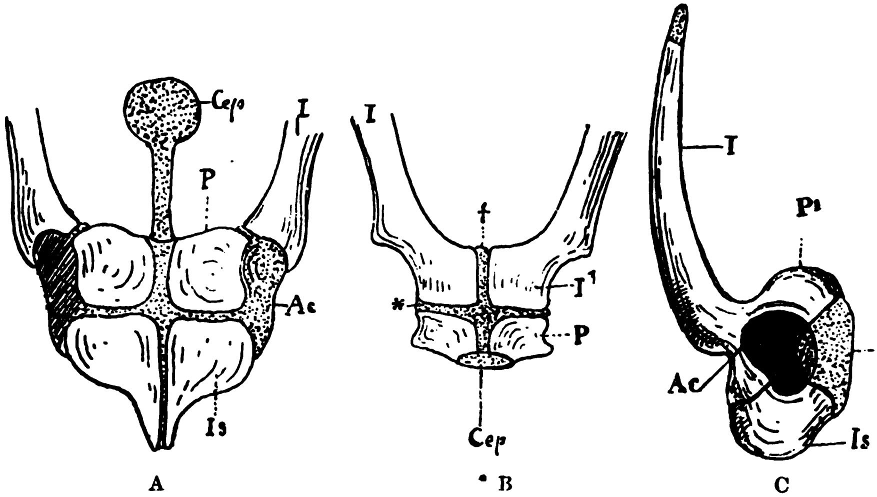


FIG. 108.—PELVIS OF ANURA. A, *Xenopus*, from below; B, the same from the front; C, *Rana esculenta*, from the right side.

Ac, acetabulum; *Cep*, epipubic cartilage; *I*, ilium; *I*¹ (in Xenopus), the proximal end of the ilium, which is separated from its fellow and from the pubis by a + -shaped zone of cartilage, †, *; *Is*, ischium; *P*, pubis (*P*¹ in *Rana*, pubic end of ilium).

One of the most characteristic differences between the pelvis of Fishes and that of Amphibians is seen in the marked development of the *iliac region* in the latter group. The ilium, like the scapula, extends upwards in the lateral walls of the body; and in Proteus and Amphiuma, owing to the reduction of the limbs in these forms, does not reach the vertebral column (Fig. 107, A, B). In all other Amphibia, as in the Amniota, it comes into connection with the sacrum, owing to the necessity for the hind-limb to act as a support for the body in terrestrial animals.

The pelvis of the Anura differs from that of Urodela in the following characteristics. In correspondence with their mode of progression, the ilium of each side becomes extended so as to form a long rod (Fig. 108, C); and the ischiopubic plate, which in Urodeles lies in the plane of the abdominal walls, becomes closely pressed together in the middle line and gives rise to a well-marked ventral keel: it is not perforated by the obturator nerve. The pubic region, moreover, though often calcified, is independently ossified only in the case of Xenopus (Fig. 108, A, B).

Reptiles.—The chief characteristics of the Reptilian pelvis as compared with that of Amphibians consist in: (1) a much more marked differentiation of the pubis, which is more distinctly separated from the ischium by an ischiopubic foramen; (2) the greater development of the ilium, which is sometimes broadened out at its vertebral end; and (3) the more intense and solid ossification of the arch as a whole.

Points of connection with the pelvis of Amphibians are seen in certain fossil forms (*e.g.* Palæohatteria, Plesiosauria), and also in Hatteria and the Chelonia. In the Plesiosauria and Hatteria (Fig. 109) the pubes are not very widely separated from the ischia, so that the ischiopubic foramina are not so extensive as in many other Reptiles.

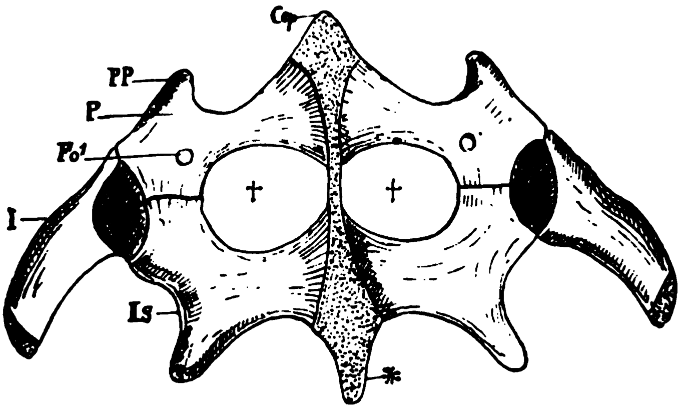


FIG. 109.—PELVIC ARCH OF *Hatteria*. (After Credner.) From the ventral side.

Cep, epipubic cartilage; *Fo*^{1}, obturator foramen; *I*, ilium; *Is*, ischium; *P*, pubis; *pp*, prepubis; *, hypoischiatic process, which becomes segmented off from the pelvis in other Reptiles. †, †, ischiopubic foramina.

From this condition that seen in the Chelonia, more especially in Macrochelys and Chelydra, may be easily derived (Fig. 110, A). In both cases the epipubis and prepubis are strongly marked. In other respects there is great variation in the form of the pelvis in Chelonians, but the obturator and ischiopubic foramina are never distinct from one another (Fig. 110).

The pelvis of the typical Lacertilia (Fig. 111) is characterised by a lightness of build. The rod-like pubis and ischium are separated from one another by a large ischiopubic foramen, and between them in the middle line is a longitudinal fibro-cartilaginous ligament, continuous anteriorly with the plug-like epipubic cartilage and posteriorly with the hypoischium or *os cloacæ* (absent in Chameleons). This tract represents the remnant of the median ends of the pubis and ischium which are present in the embryo; and thus in this, as in certain other respects, the pelvis of the Lacertilia may be said to pass through a Hatteria-like stage in the course of development. The ilium in some cases is almost vertical in position: in others it is more oblique, sloping upwards and backwards from the acetabulum.

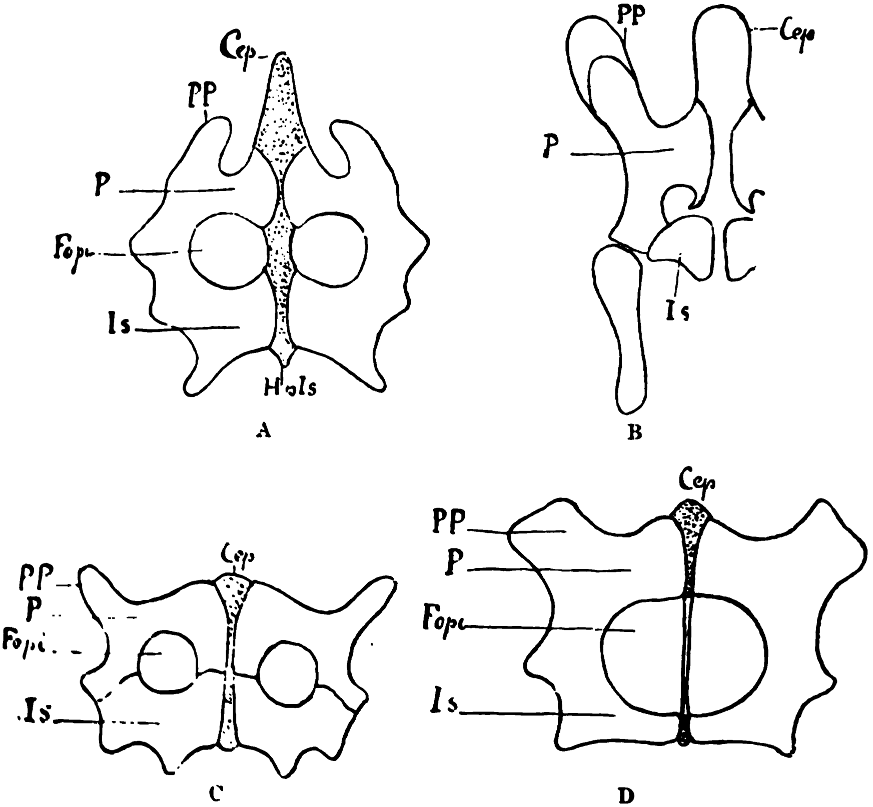


FIG. 110. PELVIC ARCH OF VARIOUS CHELONIANS. From the ventral side. A, *Macrochelys* (after G. Baur); B, *Sphargis coriacea* (after Hoffmann); C, *Testudo*; D, *Chelone*.

Cep, epipubic cartilage; *Fopi*, ischiopubic foramen; *HpIs*, hypoischiatic process; *Is*, ischium; *P*, pubis; *PP*, prepubis.

In Snake-like Lizards the pelvis undergoes degeneration, and in Amphisbænians vestiges merely of the ilium and pubis are present; in certain Snakes vestiges of a pubis alone occur.

While the pelvis of Lizards and Chelonians show a certain amount of similarity, that of Crocodiles exhibits special characteristics and is of particular interest, as in some points it resembles that of certain extinct forms. The pubes, which have at first a transverse position, become later directed forwards much more markedly than in Chelonians and Lizards, and thus the ischio-pubic foramina (in which the obturator foramina are included) are very wide, and are separated from one another by a fibrous cord

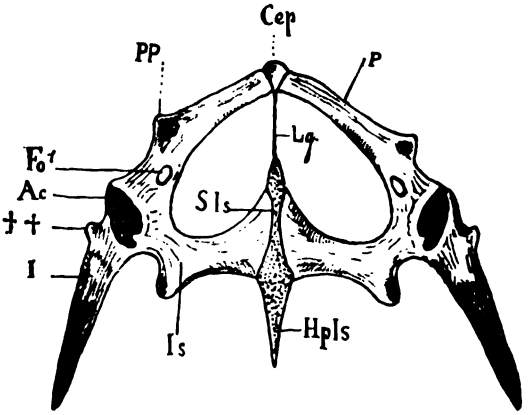


FIG. 111.—PELVIS OF *Lacerta vivipara*. From the ventral side.

Ac, acetabulum, in which the three pelvic bones come together; *Cep*, epipubis, composed of calcified cartilage; *Fo*^{1}, obturator foramen; *HpIs*, hypoischium, which becomes segmented off from the hinder ends of the ischia in the embryo as a paired structure; *I*, ilium, with its small preacetabular process ††, much more strongly developed in Crocodiles, Dinosaurians and Birds; *Is*, Ischium, forming a symphysis at *SIs*; *Lg*, fibrous ligament; *P*, pubis; *PP*, prepubis.

(Fig. 112). All three elements chondrify independently, and then unite in the acetabulum, which is perforated. The pubic bone becomes shut out from the acetabulum by a cartilaginous *pars acetabularis*, not represented in lower Vertebrates, formed from the acetabular process of the ilium. The epipubis is contained in a cartilaginous apophysis at the anterior (distal) end of the pubis, which does not, like the ischium, unite with its fellow in a symphysis: there is no hypoischium.

The ilium becomes greatly broadened out in the antero-posterior direction dorsally, where it is attached to the sacrum; a similar extension of the ilium occurs still more markedly in the Theromorpha, Dinosauria, and Birds (Fig. 113), in which it becomes connected with an increasing number of vertebræ, and so forms a firmer support to the body.

Birds.—The pelvis of Birds is chiefly characterised by the relatively large development of the iliac region and by the position of the delicate pubis, which in the course of development becomes

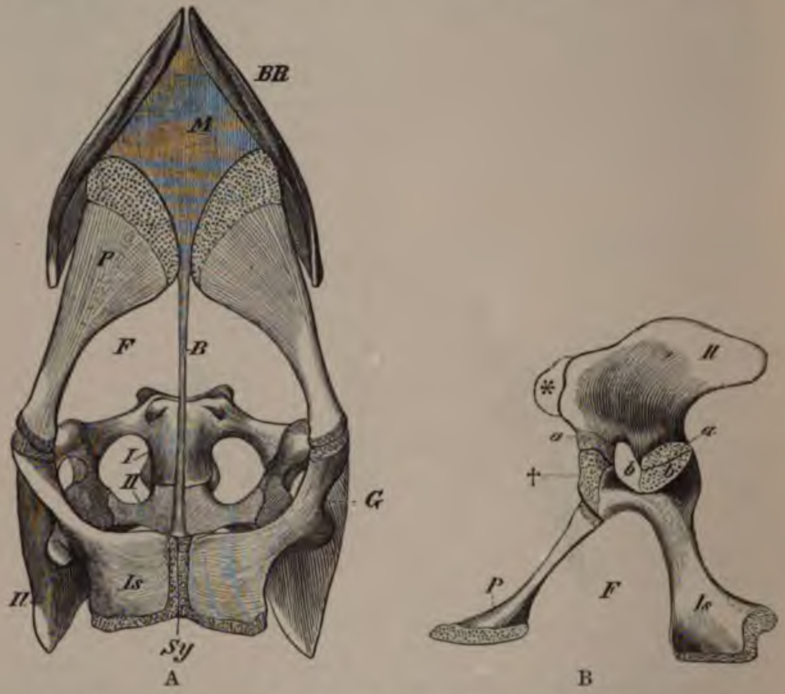


FIG. 112.—PELVIS OF A YOUNG *Alligator lucius*. A, ventral, and B, lateral view.

B, fibrous band between the pubis and symphysis ischii; *b*, foramen in the acetabulum, bounded posteriorly by the two processes, *a* and *b*, of the ilium and ischium respectively; *F*, ischiopubic foramen; *G*, acetabulum; *Il*, ilium; *Is*, ischium; *M*, fibrous membrane extending between the anterior margin of the pubis and the last pair of "abdominal ribs" (*BR*); *P*, pubis; *Sy*, symphysis of ischium; *, indication of a forward growth of the ilium, such as is met with in Dinosaurians and Birds; †, pars acetabularis, which is interposed between the process *a* of the ilium and the pubis; *I*, *II*, first and second sacral vertebræ.

directed backwards, parallel to the ischium and postacetabular process of the ilium. The preacetabular portion of the ilium extends forward for a considerable distance, and a number of vertebræ belonging to other than the true sacral region become secondarily connected with the ilium (cf. p. 60). The acetabulum is perforated, and the pars acetabularis forms a pectineal process which is retained in the adult in Apteryx (Fig. 113). The elements of the pelvis usually become ankylosed. The pubis actually meets its fellow in the middle line only in Struthio, and the ischium (dorsally) only in Rhea. A process given off from the posterior end of the pubis in the Emu, and extending forwards, may represent an epipubis.

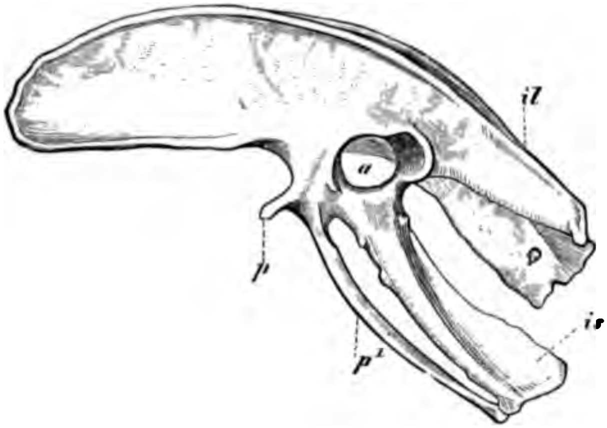


FIG. 113.—PELVIS OF *Apteryx australis*. Lateral view. (After Marsh.)

***a*, acetabulum; *il*, ilium; *is*, ischium; *p*, pectineal process from the pars acetabularis; *p*¹, pubis.**

In Archæopteryx, all the elements of the pelvis were independent and relatively small, the ilium coming into relation with about six vertebræ only, and the pubis and ischium being less backwardly directed than in recent Birds.

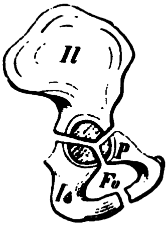


FIG. 114.—RIGHT HALF OF THE HUMAN PELVIS. LATERAL VIEW.

***Fo*, obturator foramen; the three bones—ilium (*Il*), ischium (*Is*), and pubis (*P*)—are shown distinct from one another in the acetabulum.**

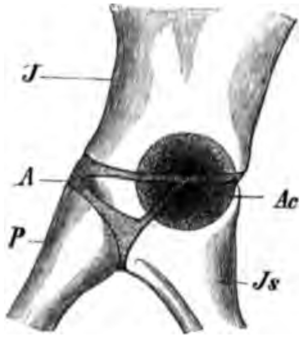


FIG. 115.—DIAGRAM SHOWING THE RELATIONS OF THE PARS ACETABULARIS in *Viverra civetta*.

***A*, acetabular bone; *Ac*, acetabulum; *J*, ilium; *Js*, ischium; *P*, pubis.**

Mammals.—The ilium and ischium of Mammals, like those of the Anura and Sauropsida, are respectively preacetabular and postacetabular in position, and the elements of the pelvis remain separated for a long time by cartilage, but later become fused (Fig. 114). The pubis always takes less part in the formation of the acetabulum than do the other two bones, and may be more or less entirely shut out from it by an ossification of the pars acetabularis, which subsequently unites with either the ilium, ischium, or pubis (Fig. 115). This *acetabular bone* is especially well developed in the Mole, in which it shuts the ilium, as well as the pubis, out of the acetabulum; in Monotremes the acetabulum is perforated. The angle between the axes of the ilium and sacrum is largest in Ornithorhynchus, and most acute in Rodents; the ilium is connected with a varied number of vertebræ in the different forms.

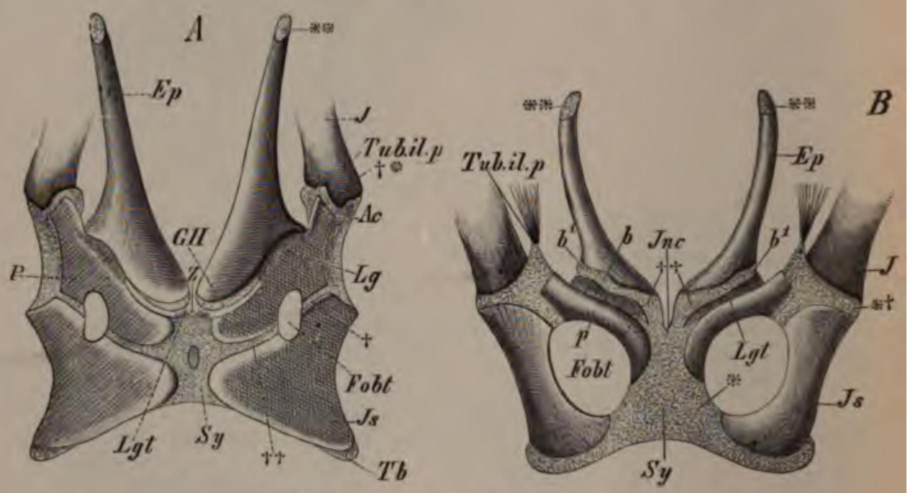


FIG. 116.—PELVIS OF A, *Echidna hystrix* (ADULT), AND B, *Didelphys azaræ* (FŒTUS, 5·5 CM. IN LENGTH). From the ventral side.

Ep, epipubis (marsupial bone); *Fobt*, obturator foramen; *J*, ilium; *Js*, ischium; *Lg* and *Lgt*, ligament between the pubis and epipubis; *P*, pubis; *Sy*, ischiopubic symphysis; *Tub.il.p*, iliopectineal tubercle; **, cartilaginous apophysis at the anterior end of the epipubis.

In Fig. A, *GH*, articulation between the pubis and epipubis; *Tb*, cartilaginous tuber ischii; *Z*, process on the anterior border of the pubis; †*, †, ††, ilio- and ischio-pubic sutures.

In Fig. B, *b*, *b*¹, cartilaginous base of the epipubis, continuous with the interpubic cartilage at †; *, *†, ischio-pubic and ischio-iliac sutures.

The original type with both pubic and ischiatic symphyses, indicating an elongated form of pelvis, is seen in Monotremes, Marsupials (Fig. 116), many Rodents, Insectivores, and Ungulates. In many other Insectivores, in Carnivores, and more particularly in the Primates, the ischia no longer meet below, and the broadening of the ilia seen in the higher forms of the last named Order culminates in Man. The greatest amount of variety in the form of the pelvis in any one order with typical appendages is seen in Insectivores, in some of which (*e.g.* Mole, Shrew), as well as in most Bats, there is no symphysis pubis, so that the relatively small pelvic cavity is not enclosed ventrally by bone. The obturator foramen is always surrounded by bone.

In the Cetacea, in which hind limbs are wanting, paired vestiges of the ischiopubic region of the pelvis are present: they are unconnected with one another and with the vertebral column. In the Sirenia, a paired bony rod (Manatus) or plate (Halicore) represents the last vestige of an ilium, in which an ischium is included in the latter genus.

In Monotremes and Marsupials of both sexes, two strong so-called "marsupial bones" (Fig. 116) arise from the anterior border of the pubes, right and left of the middle line, and extend forward in a stright or oblique direction embedded in the body-walls, serving for the attachment of muscles. They form an integral part of the pelvis, and in the embryo are seen to be in direct connection with its cartilaginous symphysis (Fig. 116, B); but later on definite articulations are formed between them and the pubes (A). It is not improbable that these structures are the homologues of the epipubis of lower Vertebrates, which has been retained in non-placental Mammals in order to serve as a support for the abdominal walls in connection with the marsupial pouch.

PAIRED FINS OF FISHES.

Fishes.

The development of the extremities has already been alluded to (p. 137). The pelvic fin usually retains a simpler and more primitive form than the pectoral fin.

Elasmobranchs.—The cartilaginous skeleton of the fins is the most richly segmented in these Fishes. There are usually two main elements (basalia) in the pelvic fin which articulate with the arch and with which a variable number of segmented rays are connected, the latter passing towards the periphery of the fin (Fig. 117). Both the larger, posterior *basipterygium* or *metapterygium*, and the smaller, inconstant *propterygium* must be looked upon as originating phylogenetically by a fusion of the proximal ends of the primary cartilaginous rays of the fin; and the form and relations of these main elements vary according to the degree in which such a fusion has taken place.[1] This is also true as regards the pectoral fin, in which an additional basal piece, or *mesopterygium*, is usually present (Fig. 99): there may even be four basalia. These complications arise in connection with the greater importance of the pectoral fin as an organ of locomotion. The distal portions of both fins are supported by horny fibres (cf. note on p. 137). With the exception of one—or at most of very few—all the rays are situated on the same side of the basalia (*uniserial* type).

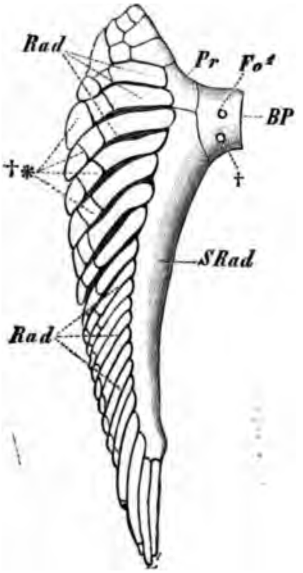


Fig. 117.—Right Pelvic Fin of *Heptanchus*. From the ventral side.

BP, pelvic plate; *Fo*¹, †, nerve-foramina; *Pr*, propterygium; *Rad*, radii, which show secondary segmentation; *S Rad*, basi- or metapterygium.

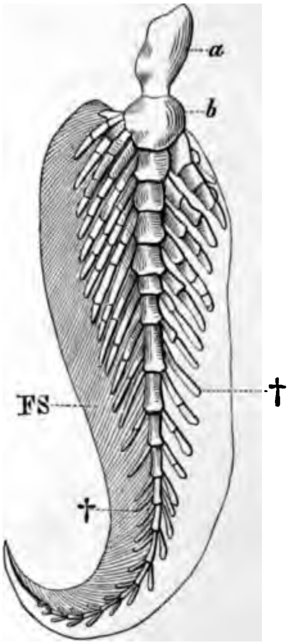


Fig. 118.—Pectoral Fin of *Ceratodus fosteri*.

a, *b*, the two first segments of the main axial ray; *FS*, dermal rays, shown only on one side; †, †, lateral rays.

In Rays, the propterygium of the pectoral fin, and usually also the metapterygium, are strongly developed, the former extending far forwards so as to be connected with the skull by ligament, and in some cases even uniting with its fellow in front of the skull.

Dipnoans.—The cartilaginous pectoral and pelvic fins are here

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[1] In male Elasmobranchii a number of pieces of cartilage are connected with the distal end of the basipterygium of the pelvic fin as a support for the copulatory organs or claspers (*q.v.*): these may become more or less calcified.

also essentially similar to one another, the latter being rather the simpler of the two. From a segmented main ray or axis a number of segmented secondary rays arise on either side in Ceratodus: these are not, however, strictly symmetrical (Fig. 118). Beyond them dermal rays are present (p. 137). A proximal (basal) segment of the axis, which bears no rays, articulates with the arch. In Protopterus and Lepidosiren the fins, with their skeleton, have undergone a marked reduction, so that little more than the segmented axis remains.

Thus the fins of Dipnoans differ from those of most Elasmobranchs (as well as of Teleostomes) in being formed on a *biserial* type, indications of which are, however, as already stated, seen in the embryos and adults of certain Elasmobranchs. Physiologically, the Dipnoan fin, like that of the young Polypterus, serves not merely as a swimming organ, but also to support the body when the animal is resting on the bottom, as do the limbs of a Urodele.

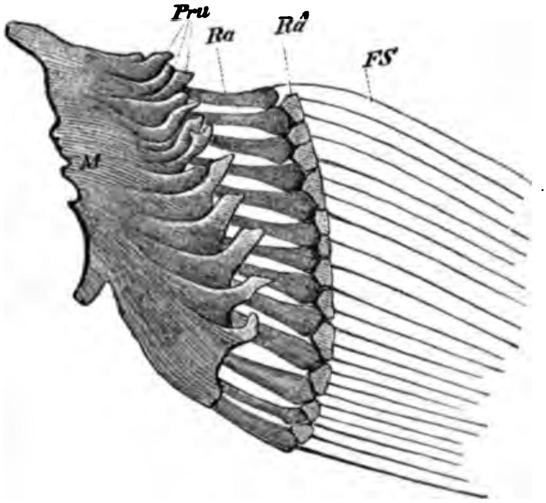

FIG. 119.—RIGHT PELVIC FIN OF A YOUNG *Polyodon folium*. From the dorsal side.

FS, bony dermal rays; *M*, metapterygium; *Pru*, uncinate ("iliac") processes; *Ra*, *Ra*¹, radii of the first and second orders.

Ganoids.—The skeleton of the fin is much simpler and the primary rays much fewer in number in Ganoids than in Elasmobranchs. This is, however, compensated for by the formation of secondary dermal bony structures, as in the case of the pectoral arch and skull: these arise on either side of the fin and may or may not be segmented: they are always more strongly developed on the anterior than on the posterior border of the fin. The most

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anterior or marginal ray comes into close connection with the cartilage of the primary fin-skeleton (Sturgeons) or entirely replaces it (Amia).

In the pelvic fin of cartilaginous Ganoids (Fig. 119) more or fewer of the radii are connected proximally with a segmented basale, which is perforated by nerves, and from which a very primitive pelvic plate may in some cases become differentiated (Fig. 104, B). It is important to bear in mind that the distinction between an axis and secondary rays cannot, therefore, be strictly recognised, as the basale corresponds to a number of fused radii, and is perhaps not comparable to the metapterygium of Elasmobranchs: but it is doubtful whether this character is primitive or secondary.

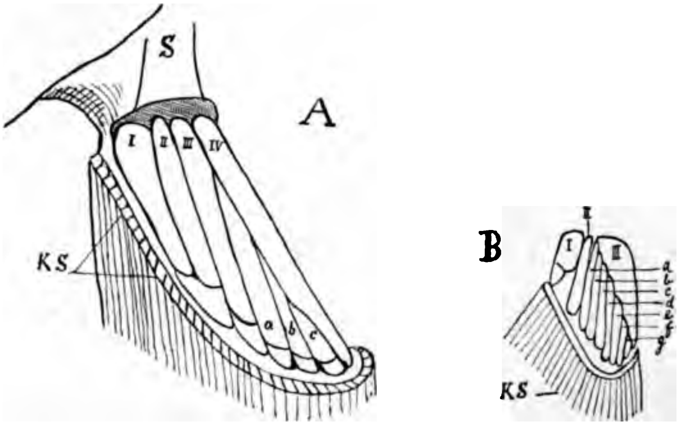

Fig. 120.—Left Pectoral Fin of A, *Polyodon*, and B, *Amia*.

a—*g*, radii which do not reach the arch and are connected with the most posterior ray (*IV.* in A, *III.* in B); *I*—*IV*, cartilaginous radii connected with the arch (*S*); *KS*, bony dermal rays.

The primitive relations have to a certain extent disappeared in the pectoral fin of cartilaginous Ganoids, which, however, also consists of a varied number of rays. Of these, four reach the arch in Polyodon (Fig. 120, A), and five in Acipenser.

In the pectoral fin of Amia (Fig. 120, B) two large converging marginal rays articulate with the shoulder-girdle, and only one intermediate ray reaches the arch: this condition may be compared with that seen in the highly-developed pectoral fin of Polypterus (Fig. 121), which is flanked on either side by a strong, ossified ray, between which is an intermediate region. The fin, therefore, resembles that of an Elasmobranch with its propterygium, mesopterygium, and metapterygium.[1]

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[1] Even if it should be proved that the intermediate region (*MS*) no longer arises in the embryo by a fusion of separate rays, it is possible that this was the case phylogenetically.

The form of the pelvic fin in Polypterus and other bony Ganoids may be easily derived from that seen in the cartilaginous representatives of this order, and it may be assumed that the basale is due to the concrescence of a larger number of separate radii, which are, therefore, much less numerous than in the Sturgeons (Fig. 104). Bony rays support the distal part of both pairs of fins (p. 137).

Teleosts.—A still further reduction has taken place in the primitive skeleton of the paired fins in Teleosts, there being at most only a few radials articulating with the arch (Fig. 100), and even these (especially in the case of the pelvic fin, in which the arch is usually considered to be undifferentiated), may be wanting. The main part of each fin is supported by bony rays, as in Ganoids. The skeleton of the fins of Siluroids, Cyprinoids, and Gymnotidæ comes nearest to that of Ganoids.

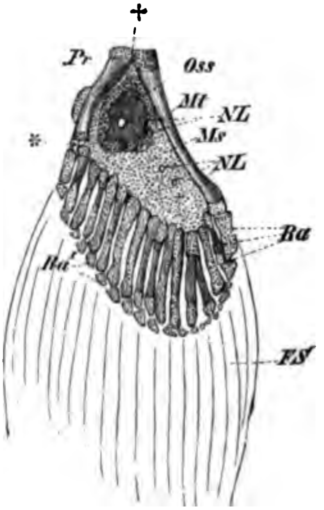

FIG. 121.—PECTORAL FIN OF *Polypterus*.

FS, bony dermal rays; *Nl*, nerve foramina; *Oss*, centre of ossification in *MS*; *Pr*, *Mt*, bony marginal rays, which meet at †, so that the intermediate region (*MS*) does not reach the arch; *Ra*, *Ra*¹, radii.

PAIRED LIMBS OF THE HIGHER VERTEBRATA.

Though it is possible to derive the skeleton of the fin of all the Orders of Fishes from a single ground-type, it is a far more difficult task to trace the connection of the latter with the extremities of Amphibia and Amniota. Between these two types of extremity there seems to be a wide gap, in consequence of the different conditions of life existing between aquatic and terrestrial Vertebrates. We do not know how the pentadactyle limb of an air-breathing Vertebrate (*cheiropterygium*), adapted for progression upon land, has been derived from the fin (*ichthyopterygium*), only fitted for use in the water, and Palæontology has so far furnished no solution to this problem.

There is, however, a certain amount of probability in the view that the cheiropterygium has arisen from such an ichthyopterygium as that seen in cartilaginous Fishes, although it is quite uncertain as to how far the individual parts are comparable to one another (Fig. 122), and how the fin, which is practically a single-jointed lever, amply sufficient for the movement of the body in a fluid medium, became gradually transformed into a many-jointed system of levers.

As the function of the limb is now no longer simply to propel the body, but also to lift it up from the ground, the firmly connected elements of its skeleton are placed at an angle to one another (elbow and knee, in which the angle is directed backwards and forwards respectively), definite articulations being formed between them in a proximo-distal direction. The fore-limb serves in typical cases mainly for pulling and the hind-limb for pushing the body along the ground, and on this fact depend the various differences between the two as regards their relation as a whole to the trunk and of their various parts to one another. Instead of projecting horizontally outwards, the limb extends downwards, and thus the angle between it and the median plane of the trunk is gradually reduced, until in Mammals eventually, the longitudinal axis of the limb, when at rest, is parallel with the median plane of the body. In the higher types this is more particularly the case as regards the posterior extremities, the anterior limbs undergoing the most varied adaptative modifications, and giving rise to prehensile or to flying organs—or, as in aquatic Mammals, becoming once more converted into paddles. The fore-limbs and hind-limbs of all Vertebrates above Fishes may, however, be reduced to a single ground-type.

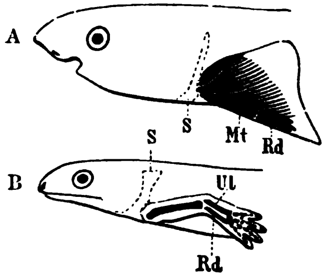

Fig. 122.—Diagrammatic Figures to show the Relations of the Anterior Extremity to the Trunk in Fishes (A), and the Higher Vertebrates (B).

Mt, metapterygium; *Rd*, radialia in A, radius in B; *S*, pectoral arch: *Ul*, ulna; proximally to *Ul* and *Rd* is the humerus.

A division into four principal sections can always be recognised: in the case of the fore-limb these are spoken of as upper arm (*brachium*), fore-arm (*antibrachium*), wrist (*carpus*), and hand (*manus*); and in the hind-limb as thigh (*femur*), shank (*crus*), ankle (*tarsus*), and foot (*pes*) (Fig. 123). The bone of the upper arm (*humerus*), like that of the thigh (*femur*) is always unpaired, but two bones are present in the fore-arm and shank. The former are called *radius* and *ulna*, and the latter *tibia* and *fibula*. The hand and foot are also respectively divisible into two sections, a proximal *metacarpus* and *metatarsus*, and a distal series of *phalanges*, which form the skeleton of the fingers and toes (*digits*).

Both manus and pes are made up of several series of cylindrical bones. There are never more than five complete series, which—except as regards number—present essentially similar primary relations throughout the higher Vertebrates. The skeleton of the carpus and tarsus, each of which typically consists of a series of small cartilages or bones, shows much variation; but the following arrangement may be taken as typical (Fig. 123).

Round a *centrale*, which may be double, is arranged a series of other elements, of which three are proximal, and a varying number (four to six) distal. The proximal, in correspondence with their relations to the bones of the fore-arm and shank respectively, are spoken of as *radiale* or *tibiale*, *ulnare* or *fibulare*, and *intermedium* ; while the distal are called *carpalia* or *tarsalia* (in the narrower sense). They are counted beginning from the pre-axial (radial or tibial) side of the limb.

Amphibians.—The anterior and posterior extremities of Urodela are formed essentially on the ground-plan described above, but more or fewer of the carpals or tarsals may undergo fusion. In them, as in Anura, there are five digits in the hind-limb, and usually only four in the fore-limb. In the Anura the radius and ulna become united, and a separate intermedium is not recognisable; the proximal row of the tarsus, moreover, consists of only two cylindrical bones, one of which (*astragalus*) corresponds to a tibiale, and the other (*calcaneum*) to a fibulare (Fig. 124).

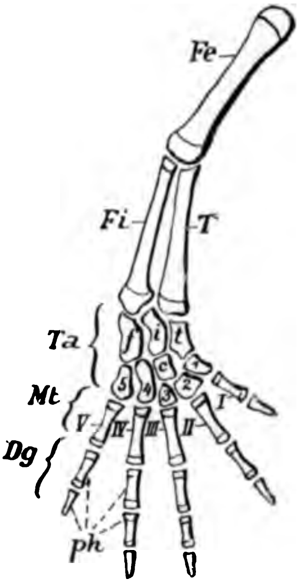

FIG. 123.—HIND LIMB OF A URODELE (*Spelerpes fuscus*).

Dg, digits; *Fe*, femur; *Fi*, fibula; *Mt*, metatarsals (*I—V*): *Ph*, phalanges; *T*, tibia; *Ta*, tarsus, consisting of—*c*, centrale; *f*, fibulare; *i*, intermedium; *t*, tibiale; and 1—5, distal tarsalia.

In the distal row of the carpus four separate elements are formed in Anura, but this number may become reduced owing to secondary fusion; in rare cases a fifth carpal may also be present. Tarsalia *II* and *III* are the most constant elements, but even these may undergo fusion, and tarsalia *IV* and *V* are generally represented by a ligament.[1]

In Anura the metatarsals and phalanges, between which the web of the foot is stretched, are, like the proximal tarsals, very long and slender. The femur, as well as the fused bones of the shank, are also exceedingly long, in correlation with the mode of progression of these animals. The skeleton of the extremities is more strongly ossified in Anurans than in Urodeles, in which many of the elements remain cartilaginous.

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[1] Very different views are held with regard to the homologies of the individual carpals and tarsals in Amphibians, and the older numbering and nomenclature are therefore provisionally retained here.

Traces of an extra element ("*prehallux*") occur on the tibial side of the tarsus, and in both Urodeles and Anurans indications

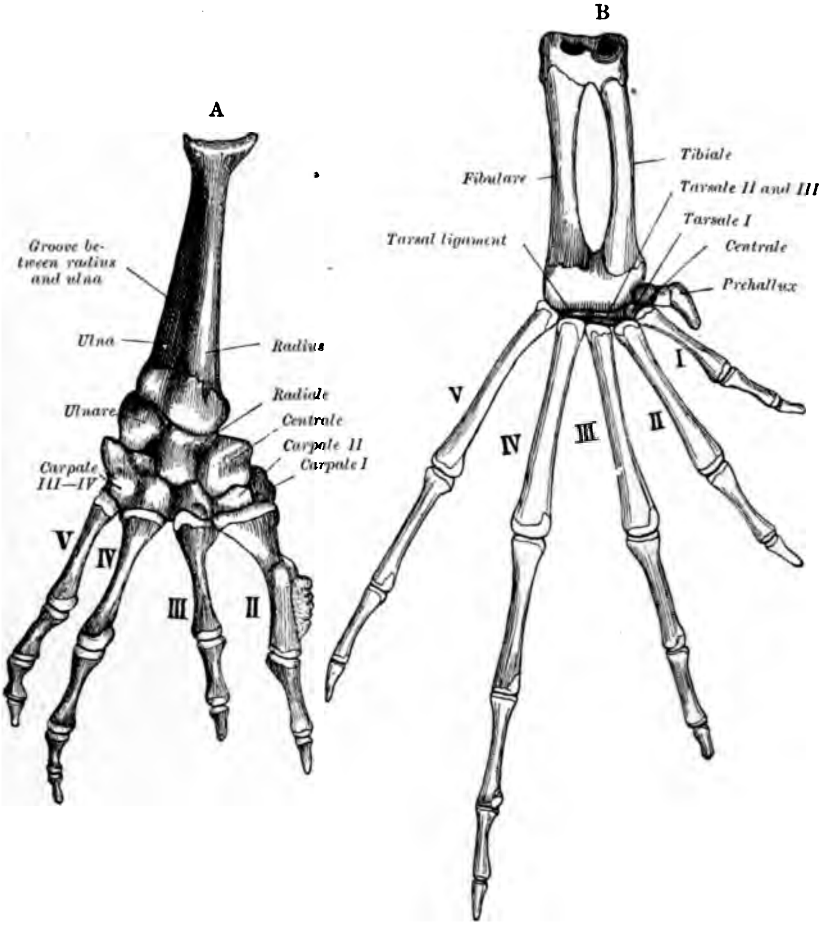

FIG. 124.—A, RIGHT FORE-ARM AND HAND, AND B, RIGHT FOOT, OF *Rana esculenta*. From the dorsal side, × 2. After E. Gaupp.

of an additional pre-axial ray in the manus are occasionally met with. The number of phalanges in the individual digits varies in different Amphibians.

Vestiges of the extremities can be recognised externally in embryos of the limbless Gymnophiona.

Reptiles.—In existing Reptiles as a general rule the body is only slightly raised from the ground in locomotion, but in some the limbs serve as more highly organised organs of support, and in certain of the Dinosauria the hind limbs were the main organs of progression. The fore limbs in such cases tend to take on other functions, and in the flying Pterosauria the fifth finger was produced into a long, jointed rod which supported a wing-like expansion of the integument.

Chelonians, and more particularly Hatteria, come nearest to the Urodeles in the structure of the carpus.[1] Five digits are usually present in Reptiles in both manus and pes, and traces also of the former possession of an extra ray both on the radial and ulnar side ("pisiform") can usually be recognised (Figs. 125—130). The tibia and fibula always remain separate.

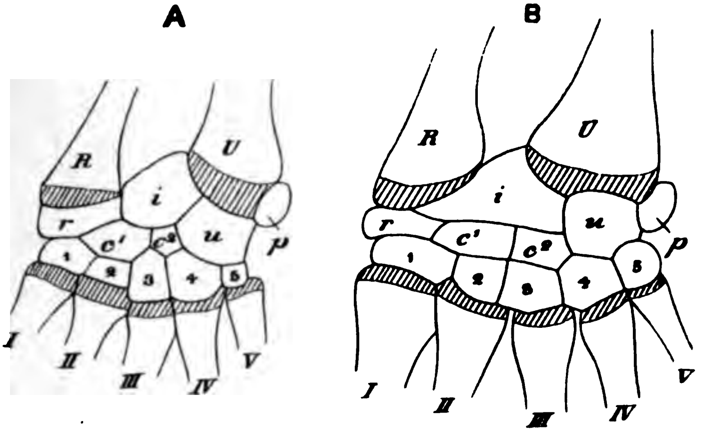

FIG. 125.—CARPUS OF A, *Hatteria punctata*, AND B, *Emydura krefftii*. (After Baur.)

c^1, radial centrale; c^2, ulnar centrale; *i*, intermedium; *p*, ulnar sesamoid (pisiform); *R*, radius; *r*, radiale; *U*, ulna; *u*, ulnare; 1—5, carpalia; *I*—*V*, metacarpals.

In Lizards and Crocodiles the carpus and tarsus diverge more from the primitive form. In the latter, which, like Anurans, possess no trace of an intermedium, the proximal row of the carpus consists of two hour-glass-shaped bones—a larger radiale, and a smaller ulnare (Fig. 128). The centrale, as in Anura, comes to be situated in the distal row, which, like the fourth and fifth digits, is much reduced.

In Ichthyosaurus and Plesiosaurus the limbs were modified to

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[1] In Hatteria and certain Chelonians, as well as in the extinct Proterosaurus, a double centrale is present in the carpus, and more or less distinct traces of a double condition of this element are seen in certain other Chelonians. Indications even of a third centrale occur in Hatteria.

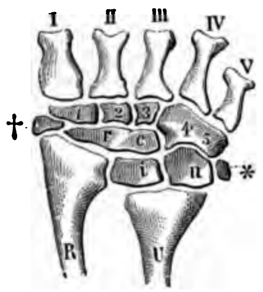

FIG. 126.—RIGHT CARPUS OF *Emys europæa*. From above.

i, intermedium; *R*, radius; *r.c*, fused radiale and centrale; *U*, ulna; *u*, ulnare; † and *, elements on the radial and ulnar side respectively, indications of additional radial and ulnar (pisiform) rays; 1—5, the carpalia, of which 4 and 5 are fused; *I*—*V*, metacarpals.

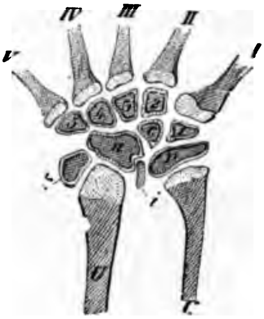

FIG. 127.—LEFT CARPUS OF *Lacerta agilis*. From above.

c, centrale; *i*, intermedium; *R*, radius; *r*, radiale, formed by the fusion of two elements, one of which corresponds to a prepollex; *U*, ulna; *u*, ulnare; †, pisiform; 1—5, carpalia; *I*—*V*, the metacarpals.

form paddles: the radius and ulna were very short, and there were numerous phalanges[1] (cf. Cetacea), additional rays being present in the former genus.

Amongst the snake-like kinds of Lizards, various degrees of

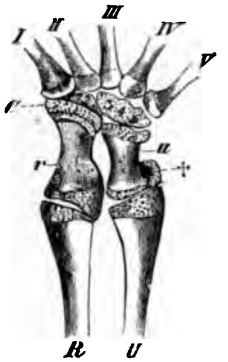

FIG. 128.—RIGHT CARPUS OF A YOUNG *Alligator lucius*. From above.

C, centrale; *R*, radius; *r*, radiale; *U*, ulna; *u*, ulnare; †, pisiform; 1 to 5, the five carpalia, as yet unossified, of which 1 and 2, as well as 3, 4, and 5, have become fused; *I*—*V*, metacarpals.

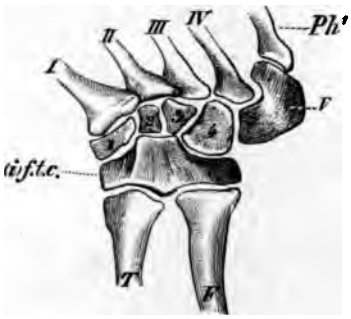

FIG. 129.—RIGHT TARSUS OF *Emys europæa*. From above.

F, fibula; (*i*)*f.t.c*, the fused intermedium(?), fibulare, tibiale, and centrale; *Ph*^{1}, phalanx of 1st digit; *T*, tibia; 1—4, distal tarsals; *I*—*V*, metatarsals.

reduction of the extremities occur, and in such forms as Anguis and Amphisbæna they have practically disappeared entirely, as in most Snakes. In certain of the latter, however, traces of the hind limbs exist (*e.g.* Python).

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[1] An indication of this condition is seen in the embryo Crocodile.

The tibia gradually becomes of relatively greater size than the fibula in the reptilian series. The tarsus always undergoes a marked reduction, especially in its proximal portion, and gradually leads to the type seen in Birds. Thus in Chelonians and Lizards (Figs. 129 and 130) the proximal tarsals may all run together into a single mass, which in the former corresponds to the tibiale, intermedium, fibulare, and centrale. In Lizards a centrale can no longer be recognised, even in the embryo, and there is no distinct trace of an intermedium. In the distal row three or four separate tarsals are developed, but these may unite with one another to a greater or less extent, and there is an increasing tendency for the movement of the foot to take place by means of an *inter-tarsal* articulation, as in the Dinosauria and also in Birds.

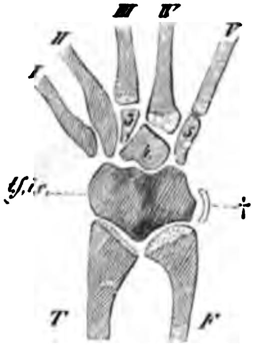

FIG. 130.—RIGHT TARSUS OF *Lacerta muralis*. From above.

F, fibula; *T*, tibia; *t.f.i.c*, fused tibiale, intermedium, fibulare, and centrale; †, trace of a 6th ray present in Geckos; 3—5, distal tarsals; *I*—*V*, metatarsals.

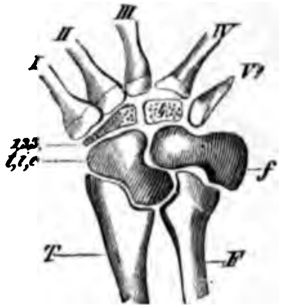

FIG. 131.—RIGHT TARSUS OF CROCODILE. From above.

F, fibula; *f*, fibulare (calcaneum); *T*, tibia; *t,i,c*, astragalus, corresponding to fused tibiale, intermedium, and centrale; 1, 2, 3, fused 1st—3rd distal tarsals; 4, 4th distal tarsal; *I*—*IV*, metatarsals; *V*?, 5th tarsal and metatarsal.

In Crocodiles (Fig. 131) there are two bones in the proximal row of the tarsus, one of which corresponds to a tibiale, intermedium, and centrale, the other to a fibulare. The former is spoken of as the *astragalus*, the latter as the *calcaneum*, and on it a definite heel (*calcaneal process*) is seen for the first time in the animal series. The distal row consists originally of four small cartilages, but these later undergo a partial fusion.

Birds.—In consequence of the fore limb of Birds having become adapted for flight, the manus loses its primitive character and undergoes reduction, while the humerus and the bones of the fore arm—more particularly the ulna, as well as the entire pectoral arch and sternum, are extraordinarily developed, the wings in good fliers being considerably longer than the legs, which alone bear the entire weight of the body when on the ground (Fig. 132). In Cursorial Birds (Ratitæ), however, the wing has undergone regressive changes in connection with their habits,

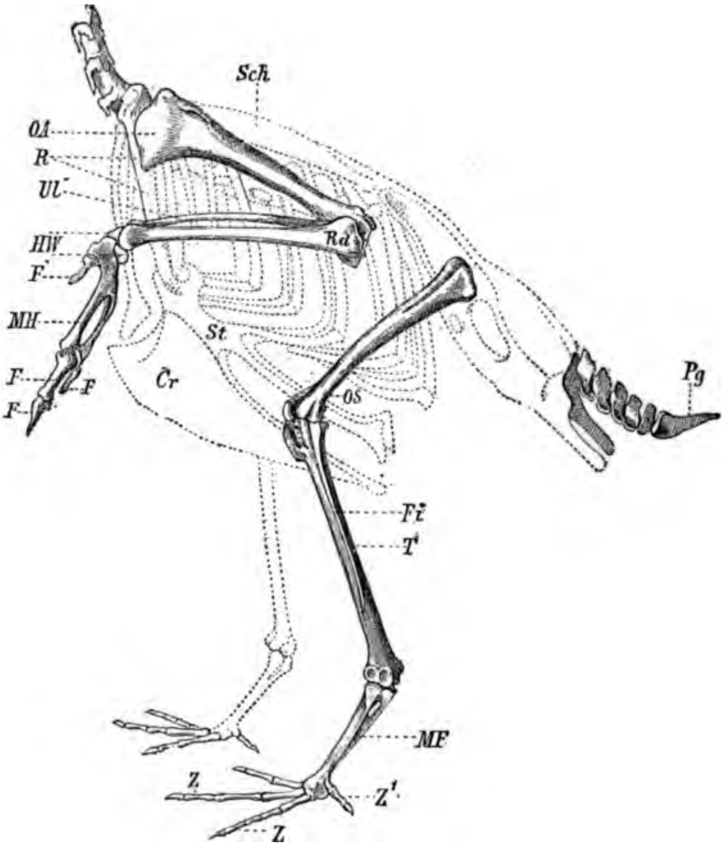

FIG. 132.—SKELETON OF THE LIMBS AND TAIL OF A CARINATE BIRD. (The skeleton of the body is indicated by dotted lines.)

F, digits; *Fi*, fibula; *HW*, carpus; *MF*, tarsometatarsus; *MH*, carpometacarpus; *OA*, humerus; *OS*, femur; *Py*, pygostyle; *R*, coracoid; *Rd*, ulna; *Sch*, scapula; *St*, sternum, with its keel (*Cr*); *T*, tibiotarsus; *Ul*, radius; z^1, z, digits.

and in the extinct New Zealand Moa (Dinornis) no trace of it has been found: in Penguins it serves as a paddle.

The relation of the superficial surface of the wings to the weight of the body is far from constant, and depends largely on the relative power of flight; on the whole, the wings are relatively *largest in* small, light Birds than in large, heavy ones.

In the carpus, at least seven elements are recognisable. In the proximal row is an intermedio-radiale and a centro-ulnare, each of which consists of two parts in the embryo. In the distal row there are also two elements, one of which (carpale 2 + 3) is evidently primarily double: the other corresponds to carpale 4. In early stages four distinct metacarpals can be seen, and these seem to correspond to the 2nd-5th rather than to the 1st-4th: the 5th metacarpal soon fuses with the 4th (Fig. 133).

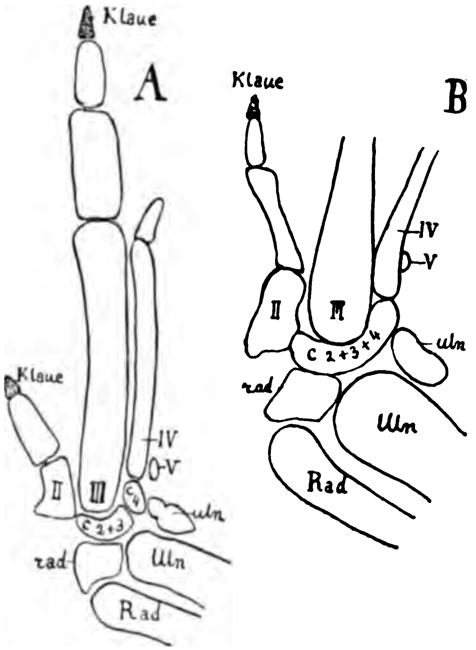

FIG. 133.—CARPUS OF EMBRYO OF *Sterna wilsoni*. A, STAGE AT WHICH OSSIFICATION BEGINS; B, STAGE IMMEDIATELY BEFORE HATCHING. (After V. L. Leighton.)

c, distal carpals; *Klaue*, claw; *Rad*, radius; *rad*, intermedio-radiale: *Uln*, ulna; *uln*, centro-ulnare; *II*–*V*, metacarpals (in B, *IV* and *V* have become fused).

The distal carpals become fused with the corresponding metacarpals, thus forming a *carpometacarpus* (Figs. 132, 133), and in the adult only the two proximal elements remain separate as a radiale and an ulnare. The three metacarpals themselves become united proximally, and the second (*III*) and third (*IV*) distally: they only bear a limited number of phalanges at their free ends.

Claws were present on the terminal phalanges of all three digits in Archæopteryx (Fig. 49). In certain recent adult Birds (*e.g.* Chauna) the first digit (*II*) bears a claw, and more rarely

(Ratitæ) the second (*III*), and even the third (*IV*) also (*e.g.* Struthio). Claws may be present in the young only (*e.g.* Opisthocomus, Sterna, Fig. 133).

The tarsus is still more reduced in Birds than in Reptiles, and consists in the embryo of three elements, two small proximal and a broader distal, which in many cases (*e.g.* Penguin) consists primarily of four distinct pieces. The former (tibiale and fibulare) unite later with the distal end of the tibia, thus forming a *tibiotarsus*, while the latter, which corresponds to tarsalia *I* to *V*, becomes included in the base of the metatarsus. Thus the foot of adult Birds no longer possesses any distinct tarsal elements, though, as in Chelonians and Lizards, it really moves by an intertarsal articulation. Of the original five metatarsals, the fifth soon disappears, while the second, third, and fourth become united with one another and with the distal element of the tarsus to form a single bone, the *tarsometatarsus* (Fig. 132), grooves at the ends of which indicate its compound nature, which is especially well seen in Penguins. The first metatarsal remains to a greater or less extent independent.

The number of toes varies between two (Struthio) and four: that of the phalanges is normally 2, 3, 4, 5, reckoning from the first to the fourth digit. The tibia, even from the first, greatly exceeds the splint-like fibula in size, and the two bones become united distally.[1]

Mammals.—In Mammals the anterior extremity either remains in the condition of a simple organ of locomotion, serving for progression on land, or it may give rise to a digging or a prehensile organ; or, again, may become modified in adaptation to an aërial (Bats) or aquatic (Pinnipedia, Cetacea, Sirenia) mode of life.

The humerus, which may possess a supracondyloid foramen near its distal end, is variously modified as regards form and relative length and the presence of ridges and elevations for the insertion of muscles; and the same is true as regards the femur and its ridges or *trochanters.*

The tibia is the more important bone of the shank, and the fibula often becomes united with it to a greater or less extent distally and sometimes proximally also, usually taking no part in the knee joint. The two shank-bones lie parallel, and are at most very slightly movable on one another (*e.g.* climbing Marsupials). The fibula never disappears entirely, but in some cases (Bats, Ruminants) only its distal end is recognisable as the lateral (external) malleolus.

The radius and ulna are connected with the humerus by a hinge-joint at the elbow, only allowing movement in one plane, and primarily their relations to one another are similar to those of the tibia and fibula. This is the case in Monotremes and in all Mammals in which the radius is fixed in a position of pronation (vide *infra*). In certain Mammals — more particularly the Primates, in which the fore limb is prehensile, the bones of the forearm, instead of being firmly connected together, articulate with one another, the distal end of the radius being capable of rotation round the ulna. When the two bones lie parallel and the wrist is not bent, the palmar surface of the manus looks inwards, and when rotated on one another towards the body, backwards: the former position is spoken of as that of *supination*, the latter that of *pronation*. Indications of these movements are seen even in climbing Marsupials.[1] The radius is the more important in supporting the hand, while the ulna forms the chief connection with the humerus. The ulna extends proximally beyond the elbow joint as the *olecranon*, on which the extensor muscles are inserted. The ulna may undergo more or less reduction and fusion with the radius, so that in some cases only the olecranon is distinguishable.

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[1] For the pneumatic character of Birds' bones, cf. under Air-sacs.

In addition to the power of rotation of the forearm, the Prosimii and Primates proper are characterised by a higher differentiation of the first finger (pollex), which becomes more independent and is capable, not only of abduction and adduction, but also of being brought into opposition with the palm of the hand to a greater or less extent. As regards the pes, the hallux even in Marsupials may be opposable, but never as markedly so as in Lemurs and Monkeys, which are often spoken of as Quadrumana.[2]

A brief account of the mammalian carpus and tarsus must suffice in this place, as considerable differences exist in the various groups, and there is no consensus of opinion as regards the homologies of the various components.

The carpus and tarsus most nearly correspond with those of Urodeles, Hatteria and Chelonians. Primarily the centrale can be recognised as a typical element in all pentadactyle Mammals; but as a rule it later becomes fused with one, or even with two, of the neighbouring carpals—generally with the radiale, less frequently with carpale 2 or 3. Occasionally indications of a second centrale are seen, which usually fuses with the intermedium (Homo). Similar fusion and shifting in relative position may also occur in other carpals and tarsals (*e.g.* radiale and intermedium). The "pisiform" corresponds to an additional ulnar ray, and not to a sesamoid.

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[1] The rotation of the radius on the ulna has doubtless come about largely owing to the gradual increased differentiation of the muscles during phylogeny; but this does not sufficiently account for the different relative positions of the two bones of the fore-arm and shank respectively. The tibia lies on the inner side of the shank, while the corresponding bone of the fore-arm, the radius, owing to secondary shifting, is external when in the position of supination. The reason of this cannot be due to a rotation of the distal end of the humerus, for even in Amphibians the same conditions are plainly seen. The crossing of radius and ulna has rather resulted in consequence of the manus becoming rotated in a contrary direction to that of the limb as a whole as it extends inwards towards the body in order to act as a support for the latter. Consequently, the originally parallel position of the two bones of the forearm is not retained, as it is in the case of those of the shank, in which the rotation follows the same direction as that of the entire limb.

[2] In the Marmosets (Arctopithecini) the thumb is not opposable, and the opposable hallux is the only digit which bears a flat nail, all the others having claws. In Ateles the pollex is vestigial and possesses only a single small phalanx, while in Colobus it may even be wanting. In consequence of the erect position of Man, and of the foot being used merely as an organ of support and locomotion, the prehensile character of the pes has become lost.

In the tarsus the centrale (*navicular*) is retained, and is usually situated on the inner (tibial) border: it may be primarily double. The astragalus possibly corresponds to the tibiale and intermedium, and the calcaneum to the fibulare, while the *cuboid* represents tarsalia 4 and 5.

Traces of a "prepollex" and "prehallux" are present in all pentadacyle Mammals, especially in lower forms, in which they may each consist of two or more elements: in the higher Mammals there is never more than one such bone, which usually becomes fused with its neighbours.[1]

There are typically five complete digits on each foot, but this number may be reduced, the disappearance taking place in the following order,—1, 5, 2, 4: thus in the Horse the third is the only complete digit remaining (Fig. 134). The number of phalanges is similar in both hand and foot: in the first digit there are only two, while in the others there are three. An exception to this rule is seen in Cetacea, in which the phalanges are numerous. The short humerus is enclosed in the body-wall in Toothed Whales, which possess five digits, the fourth of which commonly bifurcates in the embryo; Whalebone-Whales possess only four digits.

It is interesting to trace the reduction which has taken place in the feet of the true Ungulates in the course of time. This order has been undoubtedly derived from that of the Carnivora, the fossil Condylarthra from the American Eocene and the tritubercular Creodonta from the Cretaceous forming connecting links between the two. In the Eocene, the Ungulata vera diverged into two groups, the Perissodactyla (Tapir, Rhinoceros, Horse) and Artiodactyla (Pigs, Hippopotami, Ruminants). In Fig. 134 sketches of the stages in the phylogenetic development of the fore-foot of the Horse are given, showing how it has been gradually derived from a tetradactyle form: the embryo passes through these stages in the course of its development. While in this case the third digit becomes greatly enlarged relatively

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[1] Different views have been expressed as to the morphological nature of the prepollex and prehallux, which in consequence of functional adaptation may undergo further development in some Mammals (*e.g.* Talpa). It is not possible in all cases to make a satisfactory comparison between individual elements of the carpus and tarsus, or to homologise the so-called "accessory elements."

(*perissodactyle form*),[1] and eventually is the only complete one remaining, in cloven-footed Ungulates the third and fourth digits are both functional and equally strongly developed (*artiodactyle form*, Fig. 135); their metacarpals may be united with one another and with the vestiges of the proximal ends of the second and fifth to form a "cannon-bone," while the other digits are gradually reduced. A similar reduction takes place in the hind-foot, and is here as a rule more rapid.

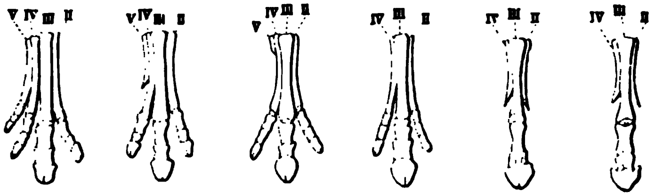

FIG. 134.—FORE-FOOT OF ANCESTRAL FORMS OF THE HORSE. 1. OROHIPPUS (Eocene). 2. MESOHIPPUS (Upper Eocene). 3. MIOHIPPUS (Miocene). 4. PROTOHIPPUS (Upper Pliocene). 5. PLIOHIPPUS (Uppermost Pliocene). 6. EQUUS.

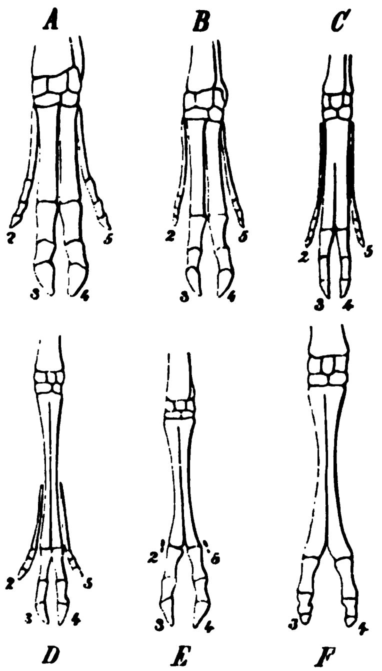

FIG. 135.—SKELETON OF THE LEFT FORE-LIMB OF *A*, PIG; *B*, HYOMOSCHUS; *C*, TRAGULUS; *D*, ROEBUCK; *E*, SHEEP; *F*, CAMEL. (From Bell, after Garrod.)

The Protungulata must originally have been pentadactyle and *plantigrade* (*i.e.* the whole foot rested on the ground) or semi-plantigrade, with ungual phalanges but little broadened. On the gradual elongation and straightening out of the limbs and unequal development of the digits, they become *digitigrade* (as in most Carnivora), and eventually *unguligrade*, only the hoofs at the extremity of the distal phalanges bearing the weight of the body.

The Tylopoda, as well as Elephants (Subungulata) have not reached the unguligrade stage: they are practically digitigrade, a large integumentary pad or sole (cf. Fig. 24), from which the small "hoofs" project, bearing the main weight of the body (Fig. 136).

Some of the many other adaptive modifications of the limbs in

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[1] The Tapir has four digits on the fore-foot and three on the hind-foot; the Rhinoceros has three on each foot.

Mammals must also be briefly mentioned. In Bats, the phalanges are greatly elongated to support the wing-membrane; the fore limbs are modified for digging in certain Mammals (*e.g.* Echidna, Mole); and in the Cetacea (cf. p. 170) and Sirenia the digits are not free, and serve as supports for the fin-like paddles. Hind limbs are absent in the two last-mentioned orders (cf. p. 155), but indications of them can be seen even externally in very young embryos of the Porpoise. In the leaping Jerboa (Dipus), the metatarsals are much elongated, and may even become ankylosed, as in Birds.

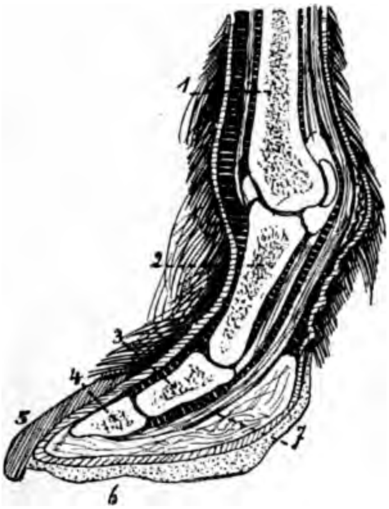

FIG. 136. — LONGITUDINAL SECTION THROUGH THE MANUS OF THE LLAMA (*Auchenia*). (After M. Weber.)

1, metacarpal; 2, 3, 4, phalanges; 5, so-called "hoof"; 6, horny part of sole; 7, cushion composed of elastic connective tissue (more strongly developed in the Elephant, in which also the phalanges are more vertical).

A bony knee-cap or *patella*, such as occurs in certain Lizards (*e.g.* Varanus) and in Birds, is present in most Mammals, being wanting only in Cetacea, Sirenia, Cheiroptera, and some Marsupialia. It has no genetic connection with the bones of the thigh and shank, and so is in no way comparable with the olecranon of the ulna, as was formerly supposed. It is a true sesamoid bone, such as occurs in connection with many of the individual joints of the digits, which has arisen in the tendon of the quadriceps femoris muscle in consequence of the friction between this tendon and the condyle of the femur.

C. MUSCULAR SYSTEM.

THE muscles, commonly spoken of as "flesh," may be divided into two groups, according to the histological character of their elements, which consist of cells elongated to form contractile fibres: namely, into those with *smooth* and those with *transversely-striated* fibres. The former are phylogenetically the older, and are to be looked upon as the precursors of the latter. The action of both in causing movements is dependent on the nervous system, a nerve entering each muscle at a definite point.

The smooth or *involuntary* muscle-fibres preponderate in the viscera, derm, and vessels, and are not under the control of the will; the striated muscles occur chiefly in the body-walls and organs of locomotion, and are almost without exception under the control of the will (*voluntary* muscles).[1] The following general statements refer exclusively to the latter kind of muscles, which may, according to their mode of development, be arranged in the following groups:—

I. **Parietal muscles** derived from the mesodermic somites.	a. *Muscles of the trunk,* including the coracohyoid of Fishes (=sternohyoid) and its derivatives in higher Vertebrates: these represent the oldest and most primitive part of the muscular system. b. *Muscles of the diaphragm.* c. *Muscles of the extremities.* d. *Eye-muscles.*
II. **Visceral muscles,** derived from the lateral plates of the mesoderm.	*Cranial muscles,* with the exception of those included under *a* and *d* above.

In its simplest form an *origin,* a *belly,* and an *insertion,* may be distinguished in each muscle. The muscles of the trunk are as a

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[1] Exceptions are seen in the muscles characteristic of the heart, and in those of the alimentary canal in the Tench. More or less of the anterior part of the digestive canal may contain striated fibres in various Vertebrates.

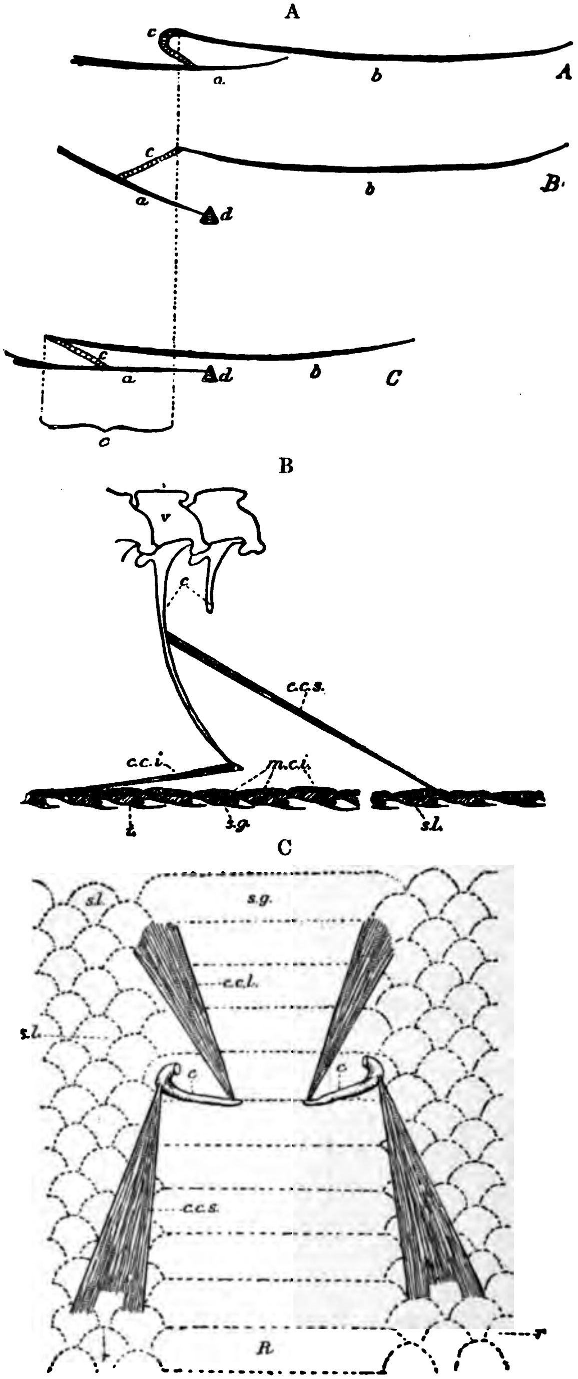
A
c
a.
b
A
c
a
d
b
B
c
a
d
b
C
c
B
v
c
c.c.s.
c.c.i.
m.c.i.
i.
s.g.
s.l.
C
s.l.
s.g.
c.c.l.
s.l.
c
c
c.c.s.
R
r

FIG. 137.—A—C. (After P. Buffa.)

A, Diagram showing the various phases in the movement of the scutes in Snakes. *a* and *b*, two consecutive scutes; *c*, the intervening integument; *d*, fixed point at free margin of scute; *e*, distance along which the scute *a* is moved; *A*, resting stage; *B*, stage in which *a* is raised and in which there is the greatest forward extension of the skin (*c*), while the free margin of the scute catches against the ground; *C*, stage in which the scute *a* again takes on a horizontal position, the skin (*c*) shows the greatest backward extension, and the scute *b* is moved forwards along the distance *e*.

B, Semi-diagrammatic figure of a longitudinal section through the ventral and lateral parts of the skin of *Tropidonotus natrix*, and of the costo-cutaneous muscles in connection with the rib. *c*, rib; *c.c.i*, *c.c.s*, inferior and superior costo-cutaneous muscle; *m.c.i*, intrinsic musculature of the skin; *s.g*, longitudinal sections of ventral scutes; *s.l*, transverse sections of lateral scutes; *v*, vertebra.

C, Inner side of part of the ventral integument of *Tropidonotus natrix*. The intrinsic muscles of the skin are not indicated. *c*, a pair of ribs with the corresponding inferior (*c.c.l*) and superior (*c.c.s*) costo-cutaneous muscles; *R*, free raised border of the ventral (*s.g*) and *r* of the lateral (*s.l*) scutes.

rule flat, while those of the extremities have usually an elongated, cylindrical, or prismatic form. In some cases, however, they assume the most varied shapes; for instance, there may be more than one origin (bicipital, tricipital, or quadricipital forms), the belly may be double (biventral or digastric form), or the muscle may be saw-shaped, or have its fibres arranged in a single or double series like the barbs of a feather.

Most of the muscles are separated by fibrous sheaths, or *fasciæ*, and may be continuous with *tendons* for connecting the muscles to the skeleton, or with flattened membranous expansions (*aponeuroses*). Wherever marked friction occurs, ossifications (*sesamoids*) may be developed in the course of a muscle or tendon.

The differentiation of independent muscles may take place—(1) by the separation of the originally single muscle into proximal and distal parts by the formation of an intermediate tendon; (2) by the splitting of a muscular mass into layers; (3) by a longitudinal splitting; or (4) by a fusion of primarily distinct muscles. A muscle may undergo very considerable modification both in form and position by a change of origin and insertion; and when the action of a muscle becomes unnecessary, it either disappears, or what remains of it contributes to the strengthening of a neighbouring muscle.

The most important point in determining the morphological value of a muscle is its nerve-supply; but other factors must also be taken into consideration—*e.g.* the homologies of the parts of the skeleton, and the relative positions of the neighbouring parts.

Integumentary Muscles.

While most muscles have intimate relations to the skeleton, which usually forms their points of origin and insertion and on which they act directly, certain others are found in the derm or subdermal connective tissue, in which they end and usually also arise: these are known as *integumentary muscles*, the first traces of which are seen in the Anura. Their relations to the integument have apparently been acquired secondarily, and they are to be looked upon, at any rate in the Amniota, as originating from true skeletal muscles: this is most plainly indicated in Monotremes (Fig. 138), in which there is a close connection between the epidermic exoskeleton and marsupial and mammary apparatus on the one hand, and the integumentary musculature on the other.[1]

Apart from the cutaneous striated muscles of the trunk and limbs, an apparatus composed of smooth muscle-fibres is present in Urodeles, and is more highly developed in Reptiles, in connection with the nostrils, serving as dilators and constrictors. In Anurans these muscles have become reduced, and play only a subsidiary part, the movements of the alinasal cartilages here depending upon those of the lower jaw, which presses upon the movable premaxillæ and thus effect the closing of the nostrils: their opening is due essentially to the elasticity of the parts. The only other integumentary muscles amongst the Anura, apart from a superior labial muscle composed of smooth elements, are certain bands in the regions of the trunk (*cutaneus pectoris*, *c. abdominis*) and thigh (*gracilis minor*), and these are only present in the higher forms.

In the Sauropsida the integumentary muscles play a great part owing to their relations to the scutes, scales, and feathers; and those of Snakes will now be briefly dealt with as an example.

Considerable variations in arrangement, form, and insertion of the integumentary muscles occur amongst the Ophidia. These differences depend mainly on the number, form, and arrangement of the ventral and lateral scales or scutes, and on the manner in which they are utilised in locomotion according to the habits of the snake in question. The muscles of the skin are most markedly developed in those snakes which can creep rapidly over the ground or burrow under it, and in which, by erection of the ventral scutes, firm points of contact are formed between the hinder edges of the latter and the ground, so that the body can be pulled or pushed forwards (Fig. 137, A).

The muscles extending from the ribs to the scutes also aid in progression; they serve to throw the body into curves and to straighten it, to draw it forwards over the integument, and conversely to move the integument forwards ventrally and laterally over the body, thus aiding in giving the scutes a firm hold on the ground (Fig. 137, B, C).

The integumentary musculature reaches its greatest develop-

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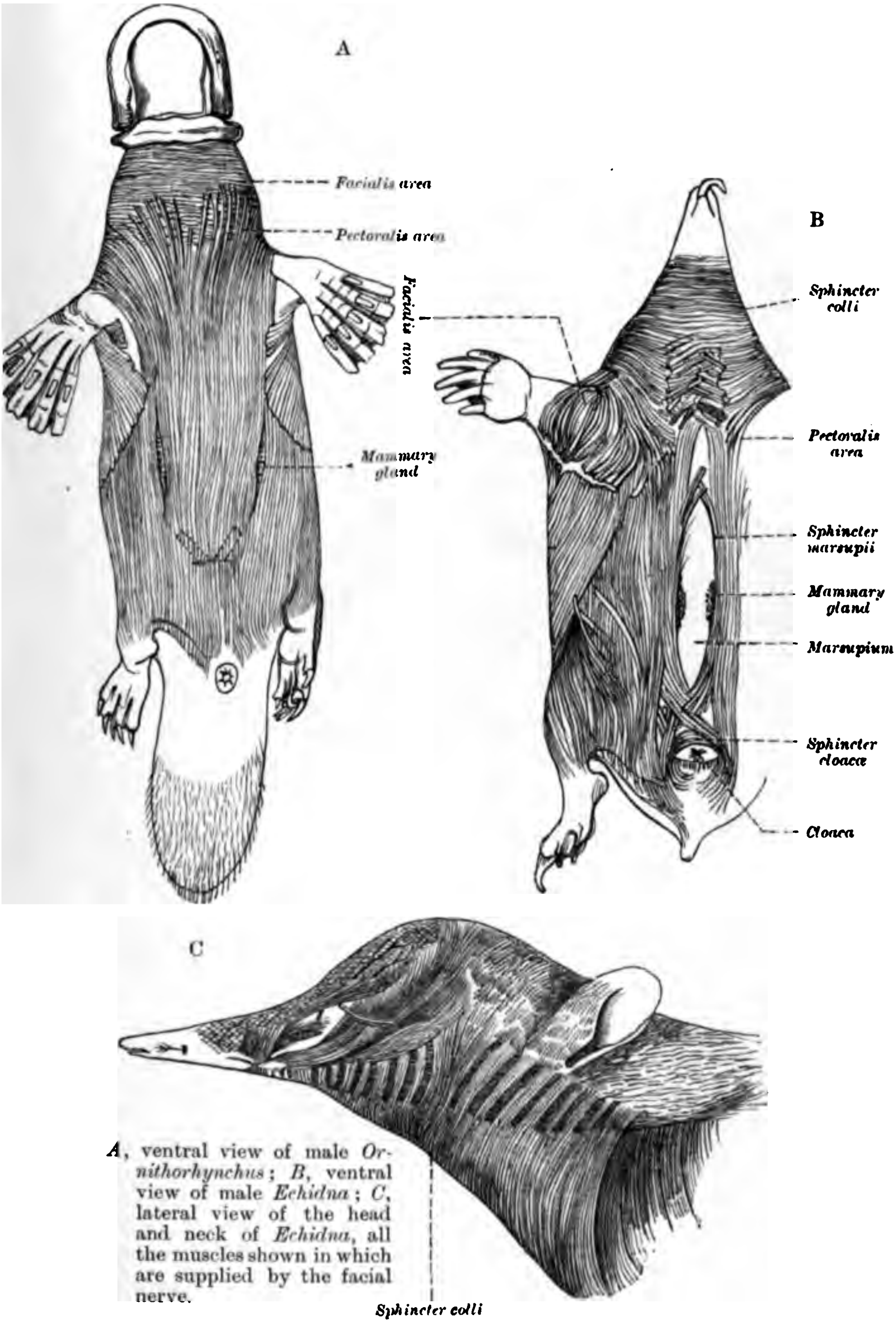
[1] It is, however, held by some Morphologists that the integumentary muscles of Reptiles and Mammals are derivatives of a superficial part of the lateral muscles of Fishes and Amphibians: in certain Anurans, Lizards, and Snakes, relations between the integument and the rectus and superficial external oblique certainly exist.



A, ventral view of male *Ornithorhynchus*; *B*, ventral view of male *Echidna*; *C*, lateral view of the head and neck of *Echidna*, all the muscles shown in which are supplied by the facial nerve.

FIG. 138.—A—C, THE INTEGUMENTARY MUSCLES OF MONOTREMES. (After Ruge.)

ment in Mammals, and exhibits numerous modifications in passing from Monotremes to Man. In lower forms (Monotremes, Fig. 138, as well as, *e.g.* Dasypus, Centetes, Erinaceus, Pinnipedia, &c.), it extends over the trunk and limbs (*panniculus carnosus*), while in Primates it becomes reduced, and confined essentially to the neck (*platysma myoides*) and head (mimetic muscles): these muscles are closely related genetically, and are all supplied by the facial nerve. Two layers can be distinguished in the platysma (Figs. 138 and 139), the more superficial of which has an oblique or longitudinal direction, while the deeper layer (*sphincter colli*) is circular: the two layers together correspond to the sphincter colli of the Sauropsida. They are continued on to the head, and there give rise to a number of new muscles which are mainly grouped around the eye, mouth, nose, and ear (Fig. 139). These mimetic muscles are most highly differentiated in Man, but at the same time reduction or tendinous transformation of certain of them takes place, and some disappear entirely.

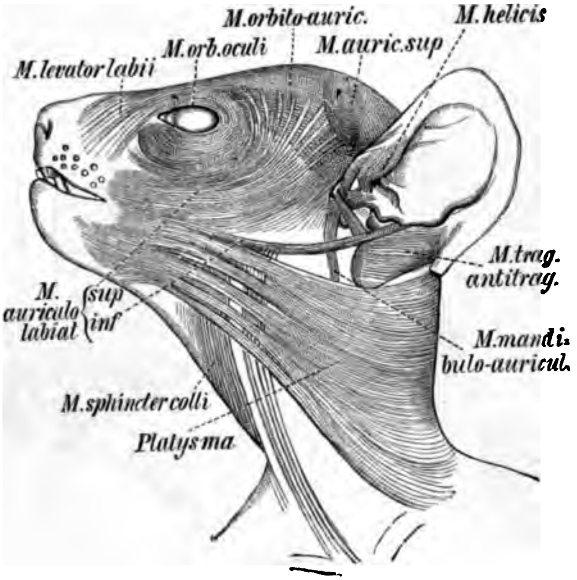


FIG. 139.—SUPERFICIAL FACIAL MUSCLES OF *Lepilemur mustelinus*. The deep layer is recognisable on the neck. (After Ruge.)

The action of the integumentary muscles is very varied in different Vertebrates. It may serve to roll up the body into a ball (*e.g.* Hedgehog, Armadillo), or aid in the movements of the limbs and tail in swimming (*e.g.* Ornithorhynchus), or serve to erect the integumentary spines (*e.g.* Echidna); or may cause local movements ("twitching") of the skin (many Mammals).

Parietal Muscles.

A. *Muscles of the Trunk.*

In **Amphioxus** the body muscles are made up of a series (60 or more) of lateral muscular segments or *myomeres* separated by >-shaped connective-tissue septa or *myocommas*, between which the fibres run longitudinally. The myomeres have an alternating arrangement on the two sides. On the ventral region of the anterior two-thirds of the body is a thin transverse sheet of fibres.

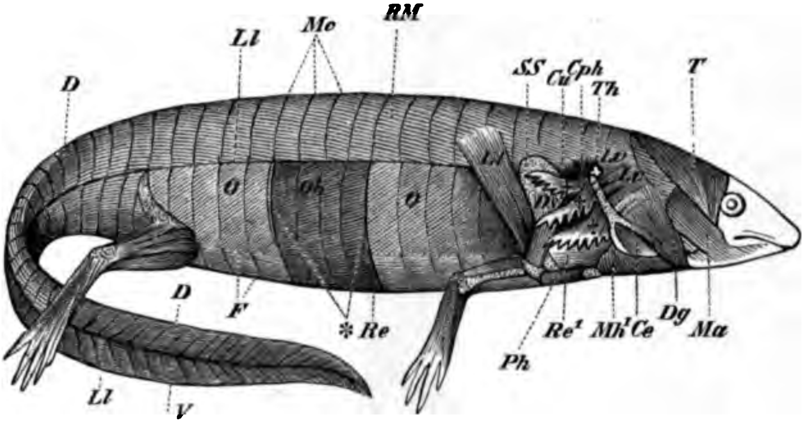


FIG. 140.—THE MUSCULATURE OF LARVAL AMBLYSTOMA (AXOLOTL). From the side.

Ce, external ceratohyoid muscle; *Cph*, cervical origin of the constrictor of the pharynx; *Cu*, cucullaris; *D*, dorsal, and *V*, ventral portion of caudal muscles; *Dg*, digastric; *Ds*, dorsalis scapulæ; *Ll*, lateral line; *Lt*, latissimus dorsi; *Lv*, levator arcuum branchialium; †††, levator branchiarum; *Ma*, masseter; *Mc*, myocommas between the myomeres of the dorsal portion of the lateral muscles; *Mh*¹, mylohyoid (posterior portion); *O*, superficial layer of the external oblique muscle, arising from the lateral line, and extending to the fascia, *F*; at * a piece of this layer is removed, exposing the deeper layer of this muscle (*Ob*); at *Re* the oblique fibres of the latter pass into longitudinal fibres, indicating the beginning of the differentiation of a rectus abdominis; at *Re*¹ the rectus-system is seen passing to the visceral skeleton; *Ph*, procoraco-humeralis; *RM*, dorsal portion of lateral muscles of the trunk; *SS*, suprascapula; *T*, temporal muscle; *Th*, thymus.

In **Fishes** the myomeres and myocommas, arising exclusively from the mesodermic somites (p. 9), have a zigzag arrangement on either side of the body, each of the former consisting, in its simplest condition, of dorsal and ventral portions, separated from one another

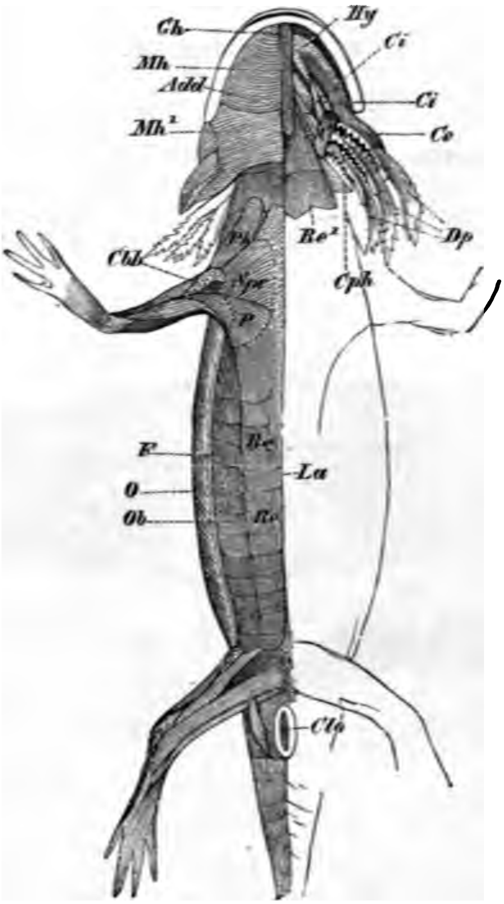


FIG. 141.—THE MUSCULATURE OF LARVAL AMBLYSTOMA (AXOLOTL). Ventral view.

Add, adductor arcuum branchialium ; *C*, constrictor arcuum branchialium ; *Cbb*, coracobrachialis brevis ; *Ce*, *Ci*, *Ci*¹, external and internal ceratohyoid : the former is inserted on to the hyoid (*Hy*) ; *Clo*, cloaca ; *Cph*, portion of the constrictor of the pharynx, arising from the posterior branchial arch ; *Dp*, depressores branchiarum ; *Gh*, geniohyoid ; *La*, linea alba ; *Mh*, *Mh*¹, anterior and posterior portions of the mylohyoid, which is cut through in the middle line, and removed on the left side, so as to show the proper visceral musculature ; *O*, superficial layer of the external oblique, passing into the fascia, which is shown cut through at *F* ; *Ob*, second layer of the same muscle ; *Ph*, claviculo-humeralis ; *Spr*, supracoracoideus ; *Re*, rectus abdominis, passing into the visceral musculature (sternohyoid) at *Re*¹, and into the pectoralis major at *P*.

by a connective tissue septum extending from the axial skeleton to the integument at the region of the "lateral line"[1] (cf. Fig. 140). The myomeres meet together in the mid-dorsal and mid-ventral lines, and constitute the great lateral muscles of the trunk.

This primitive metameric arrangement of the lateral muscles of the trunk forms a characteristic feature in Vertebrates, and stands in close relation with the segmentation of the axial skeleton and spinal nerves, the number of vertebral segments and pairs of nerves corresponding primitively to that of the myomeres.

The lateral muscles largely retain their primitive relations in Fishes, but on the ventral side of the trunk, where they enclose the body-cavity, certain differentiations occur which indicate the formation of the recti and obliqui abdominis of higher types. The dorsal portions of these parietal muscles, as well as the ventral portions in the caudal region, retain a more primitive condition.

Amphibians.—In Urodeles (Figs. 140 and 141) *primary* and *secondary* ventral trunk-muscles can be distinguished, and both of these groups, like the dorsal muscles, are segmented. The former consists of *internal obliques*, arising directly from the muscle-plate of the somite, and of *external obliques* developed from the ventral border of the myomeres; the obliqui towards the ventral middle line are connected with the *rectus abdominis.*

The secondary muscles arise by delamination from the primary, and give rise to a superficial *external oblique*, a superficial *rectus*, a *transversalis*, and a *subvertebralis.* These, however, only attain importance in caducibranchiate forms, in which they become marked during metamorphosis, and the primary musculature then undergoes more or less reduction. Thus various conditions of the ventral musculature are found amongst Urodeles.

In the broad-bodied Anura, on the other hand, both primary and secondary muscles present a marked uniformity and relative simplicity; in the adult they give rise to a segmented rectus, in part passing into a sternohyoid, a non-segmented obliquus externus, and a transversalis, as well as to a cutaneus abdominis derived from the external oblique. No trace of an internal oblique can be seen in the adult.

Reptiles.—In Reptiles, the lateral muscles of the trunk attain a much higher grade of development. This is to be accounted for by the more perfect condition of the skeleton, more especially of the ribs and pectoral arch. The ribs and intercostal muscles now play an important part in respiration, and changes, necessitated by the higher development of the lungs, are thus brought about.

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[1] This septum is not present in Myxinoids, and is absent in Petromyzon and Lepidosteus posteriorly to the gills.

The ventral muscles of Reptiles represent the primary as well as the secondary muscles of Amphibians, though differing in their further development, in consequence of which and of the course taken by the nerves, relations of the parts are seen which lead up to the condition occurring in Mammals. The primitive segmentation may be retained or more or less completely lost, in which latter case the muscles in question run together to form broad plates.

The distinction between thoracic and abdominal regions becomes gradually more plainly marked, and, in addition to the four muscular layers present in Amphibians, well-marked *external* and *internal intercostal muscles* are present: these are homologous with the primary abdominal muscles of the last-named Order, as are also the *obliquus profundus* (belonging to the system of the internal intercostals) and the median, deep *rectus abdominis.* A *transversus* is present except in Snakes. A *subvertebralis* extends from rib to rib, but is wanting in the lumbar region. A *quadratus lumborum* (lumbar portion of the intercostalis) appears first in Reptiles, and from it a *psoas major* and *psoas minor* may become differentiated.

The rectus muscle, which in Amphibia extends anteriorly to the pectoral arch and is in part continuous with the neck muscles, is in Reptiles interrupted at the sternum, so that pre- and post-sternal portions can be distinguished. The rectus abdominis is always well developed, and may consist of a segmented median and of unsegmented lateral portions: it is not strictly comparable to that of Urodeles, and the pyramidalis does not correspond to the like-named muscle of Mammals.

While no important differentiation is noticeable in the dorsal portion of the lateral body-muscles in Urodeles, a marked subdivision of these muscles is seen in Reptiles. In them may be distinguished a *longissimus,* an *iliocostalis, interspinales, semispinales, multifidi splenii,* and *levatores costarum,* together with the *scaleni,* which belong to the last-mentioned group.

The muscles of the main part of the tail retain primitive relations similar to those seen in Fishes: at the root of the tail and in the cloacal region, however, new muscles become differentiated, viz., the *ilio-, ischio-,* and *pubo-caudalis* and muscles of the anus (already indicated in Anura) and generative organs.

Birds.—In Birds the primitive character of the trunk-muscles has disappeared far more than in Reptiles. This is mainly to be accounted for by the excessive development of the muscles of the anterior extremity—the *pectoralis major*[1] more particularly—and the corresponding backward extension of the breast-bone.

External and internal oblique muscles are both present in the

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[1] The relative size of the pectoralis major does not always correspond to the power of flight. It is very compact in Carinatæ, and contains elements *corresponding to* the pectorales major and minor of Man.

abdominal region, but only slightly developed: this is more particularly true of the internal oblique, which appears to be undergoing degeneration. No trace of a transversalis can be distinguished in the abdominal region, but, on the other hand, a distinct, paired, unsegmented rectus is present, reduced anteriorly and posteriorly.

External and internal intercostals are well developed, and a *triangularis sterni* (last trace of the transversus) appears for the first time on the inner surface of the sternal ends of the ribs. The dorsal portion of the trunk-musculature is only slightly developed in the region of the body, though very strongly marked in the neck.

All these modifications in Birds seem to be accounted for by the specialisation of the mechanisms for flight and respiration, to assist which the greatest possible number of muscles are brought into play, and thereby influence the whole organism: an essential difference is thus brought about between Birds and Reptiles.

Mammals.—In general, there is a reduction of the ventral musculature in Mammals. Three lateral abdominal muscles are always present, an external and internal oblique and a transversalis. In many cases, more particularly in Tupaia and in Lemurs, the external oblique possesses tendinous intersections, thus indicating its primitive segmental character; but in general all these muscles consist of broad, uniform sheets. Towards the middle line, they pass into strong aponeuroses which ensheath the rectus abdominis The latter consists of a single band on either side and possesses a varying number of myocommas; it is no longer connected with the axial muscles of the neck belonging to the same system (*sterno-hyoid*, *sternothyroid*, &c.) as is the case in Urodeles, for the sternum is always interposed between them, as in the Sauropsida. It, however, may occasionally (*e.g.* in lower Primates) reach as far forwards as the region of the first rib: in higher forms it becomes more or less shortened, the greatest loss of myomeres being seen in Anthropoids and Man, in connection with the development and relations of the great adductor (pectoralis major) of the fore limb.

In Monotremes and Marsupials, the strong *pyramidalis* muscle lies on the ventral side of the rectus abdominis. It arises from the inner border of the marsupial bones (p. 155) and may extend forwards as far as the sternum. In the higher Mammals, in which marsupial bones are wanting, the pyramidalis usually becomes greatly reduced or entirely lost. Traces of it are, however, commonly to be met with even in the Primates, arising from the anterior border of the pubis, right and left of the middle line.[1]

The external and internal oblique muscles are represented in the thoracic region in Mammals, as in the Sauropsida, in the form of external and internal intercostals.[1] The subvertebral muscle is represented by a *longus colli* and *recti capitis antici.* What has been said above with regard to the quadratus lumborum and to the differentiation of the dorsal portion of the trunk-muscles in Reptiles applies essentially also to Mammals, in which also the metamerism of the dorsal body-wall is retained longer than that of the ventral.

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[1] A sphincter marsupii muscle is developed in connection with the marsupium (Figs. 28 and 138).

In the caudal musculature, flexors, extensors, and abductors may be distinguished, and their degree of development is proportional to that of the tail: in Man, for example, they become reduced, and some of them (the pubo- and ilio-coccygeus) have undergone a change of function, giving rise to the levator ani or "pelvic diaphragm," consisting morphologically and phylogenetically of three portions (pubic, ischiatic, and iliac).[2]

B. *Muscles of the Diaphragm.*

The formation of a *diaphragm* results from a gradual subdivision of the cœlome (pleuroperitoneal cavity) into pleuro-pericardial and abdominal portions, and the differentiation of the serous membranes which line these (*pleura, pericardium, peritoneum*) can only be understood in connection with the complicated development of the primitive urinogenital folds, liver, lungs, and great veins, and so cannot be dealt with in this place.

From the Sauropsida onwards, a more or less distinct separation of the pleural and peritoneal cavities is seen. In Chelonians and Lizards a partition is present between these chambers, but this is complete only in Crocodiles and Birds. Subperitoneal muscular elements are present which connect it with the vertebral column and ribs, but the innervation of these precludes any homology with the diaphragmatic muscles of Mammals.[3] It is here therefore only a case of analogy; and it must be remembered that in the Sauropsida the pericardium lies in the general peritoneal cavity.

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[1] The very variable *serrati postici superior* and *inferior* are peculiar to Mammals above Monotremes. They do not form a single layer, but are independent of one another, and are derived respectively from the external and internal intercostals.

[2] It is doubtful how far the external sphincter of the anus, the muscles in connection with the external generative organs, and the *transversus perinei profundus* are derivable from the original sphincter cloacæ of the Amphibia and Sauropsida. In Mammals the *pubo-coccygeus* (or the pubic portion of the levator ani), as well as the *sphincter ani externus* and *bulbo-* and *ischio-cavernosi*, are considered to represent separate portions of the integumentary muscle which primarily extended over the greater part of the trunk.

[3] Amongst the Amphibia (Rana) fibres from the transversus which extend on to the gullet have been compared to a diaphragm, but the relations are here quite different to those of the muscles of the mammalian diaphragm, in the formation of which the rectus abdominis plays an important part. In Birds, two entirely different structures have been described as diaphragms (cf. under Air-sacs).

A complete diaphragm dividing the cœlome into thoracic and abdominal cavities occurs only in the Mammalia. It is dome-shaped and muscular, its muscles arising from the vertebral column, ribs, and sternum. The diaphragm is of great importance in respiration, as it allows of a lengthening of the thoracic cavity in a longitudinal direction. It is supplied by paired phrenic nerves arising from one or more of the cervical nerves (usually the 4th or 4th and 5th, but varying from the 3rd to the 8th); and is perforated by the œsophagus, aorta, postcaval and azygos veins, thoracic duct, &c. In most cases it consists of a central tendon from which muscular fibres radiate to the periphery and form dorsally two strong "pillars" of the diaphragm. In some Mammals (*e.g.* Echidna, Phocæna) the diaphragm is entirely muscular: in the higher Primates the central tendon unites secondarily with the pericardium.

The nerve-supply of the diaphragm indicates a polymeric origin from the ventral portions of several myomeres. In the course of development, it, like the pericardium, becomes shifted backwards. The first rudiment of the diaphragm ("*septum transversum*") is composed of connective tissue into which the musculature extends secondarily, and is situated ventrally on either side of the median line: eventually it becomes closed in laterally and posteriorly.[1] It is important to note that in the innervation, as well as the grouping of the muscles, a costo-sternal and a lumbar portion can be recognised in the mammalian diaphragm.

Although in many respects the mode of evolution of the mammalian diaphragm still requires elucidation, it is at any rate certain that a close connection exists between its development and that of the thorax and the changed respiratory conditions. The diaphragm acts as an important respiratory muscle, and also aids the abdominal muscles in the compression of the abdomen.

C. *Muscles of the Appendages.*

All the muscles of the appendages of Vertebrates are primarily to be looked upon as derivatives of the ventral muscles of the trunk, *i.e.*, of the myomeres. This is indicated, apart from the nerve-supply, by their mode of development in numerous Anamnia, although in the Amniota the primitive mode of formation is not clearly recognisable owing to an abbreviation of development.

Two principal groups of appendicular muscles may always be distinguished: one lying in the region of the pectoral and pelvic arches, dorsally and ventrally, the other in the free extremity. In

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[1] This mode of formation can be recognised not infrequently in those teratological cases in which the costal and lumbar portions of the diaphragm do not become united.

Fishes the latter group consist essentially of elevators, adductors, and depressors of the fins, and these again may become differentiated into several layers. From the Amphibia onwards, in correspondence with the more highly differentiated organs of locomotion, considerable complication is seen, and there is a much more marked separation into individual muscles corresponding with the different sections of the extremity. Thus *elevators*, *depressors*, *rotators*, *flexors*, *extensors*, *protractors*, *retractors*, *abductors*, and *adductors* are present in connection with the pectoral and pelvic arches, the upper arm and thigh, forearm and shank, and hand and foot: the digits are also moved by a highly-differentiated musculature. The number of muscles gradually increases in passing from the Urodela through the Sauropsida to the Mammalia, and greatly influences the form of the skeleton.

The most important muscles of the shoulder, the origin of which from the trunk gradually becomes broader in the higher forms, are the *cucullaris*, the *sternocleidomastoideus* (belonging morphologically to the cucullaris, and, like it, supplied by the spinal accessory nerve), the *rhomboidei*, and the *levator anguli scapulæ*: these act as rotators, protractors, and retractors of the scapula.

The muscles connected with the pelvic arch cannot all be looked upon as the serial homologues of those of the more movable shoulder, for in many respects the different mechanical relations of the hind limb have caused modifications in the muscles. Thus, representatives of the *levator anguli scapulæ*, *rhomboideus*, and *serratus magnus* are not present.

A much greater similarity—especially marked in Urodeles—exists between the muscles of the free portions of the fore and hind limbs. In correspondence with the fact that the angle formed by the upper and middle sections points in opposite directions in the pectoral and pelvic limbs, the extensor muscles of the former are on its posterior border, and those of the latter on its anterior border, while the flexors have the converse arrangement. From the latter the *pronators* have arisen: these are more specialised in the fore limb than in the hind limb. The *supinators* originated from the extensors.

A very varied differentiation of the individual layers of muscle takes place in different Vertebrates in connection with the shank and foot, as well as the fore-arm and hand. The degree of differentiation of the muscles in question in general corresponds to the functional specialisations of the foot and hand, and is most marked in the hand of Primates, more especially of Man.

D. *The Eye-Muscles.*

(These will be dealt with in connection with the organ of vision.)

Visceral Muscles.

Fishes.—The visceral muscles of Fishes[1] have been most satisfactorily investigated in Elasmobranchs, and are classified by Fürbringer as follows:—

A. Cranial or cerebral muscles (consisting originally of transverse or circular fibres) supplied by the Vth, VIIth, IXth, and Xth cerebral nerves.

1. Constrictor arcuum visceralium, *incl.* constrictor superficialis dorsalis et ventralis.

	Innervation.
Levator labii superioris ,, maxillæ ,, ,, palpebræ nictitantis[2]	V.
,, rostri ,, hyomandibularis Depressor rostri ,, mandibularis et hyomandibularis	VII.
Interbranchiales	IX, X.
Trapezius	X.
2. Arcuales dorsales	IX, X.
3. Adductores, *incl.* adductor mandibulæ	V.
and abductores arcuum branchialium	IX, X.
B. Spinal muscles, originally longitudinal, and divided, like the other trunk-muscles, into myomeres.	Spino-occipital[3] and spinal nerves.
(*a*) Epibranchial spinal muscles, dorsal to visceral skeleton.	
4. Subspinalis	Spino-occipital nerves.
5. Interbasales	Spino-occipital nerves, as well as the first spinal nerve.
(*b*) Hypobranchial spinal muscles, ventral to visceral skeleton.	
6. Coraco-arcuales, *incl.* coraco-branchiales, coraco-hyoideus, and coraco-mandibularis	Spinal nerves, and partly the last one or more of the spino-occipital nerves.

In the Ganoidei, Dipnoi, Teleostei, Amphibia, and Amniota there are no epibranchial spinal muscles, and the hypobranchial muscles have a very different form from those of Elasmobranchs: in Teleosts, for instance, they are much simplified. In Amphibians, as already mentioned, the rectus system of the trunk is only partially interrupted by the sternum and pectoral arch, and is continuous with the sternohyoid. These different conditions of the muscles result from the varied adaptations of the visceral skeleton and respiratory organs.[1]

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[1] In Cyclostomes there is a remarkable transformation of the cranio-visceral musculature in correspondence with their peculiar cranial skeleton (suctorial apparatus) and branchial basket. It is covered over secondarily by the trunk muscles.

[2] This muscle has nothing to do with the other eye-muscles.

[3] These are spinal nerves emerging from the occipital region of the skull (cf. under Nervous System).

Amphibians.—It is to be expected, *a priori*, that the musculature of the visceral skeleton should be more highly developed in branchiate than in air-breathing Amphibians; in the former, more primitive relations are met with, while in the latter a greater modification, or rather reduction, of these muscles takes place.

The muscles of the hyoid and branchial arches may be divided into three groups—a dorsal (*levatores arcuum*), a middle (muscles of the external gills and the *external ceratohyoid*), and a ventral (*internal ceratohyoid*, *subarcuales*, and interbranchialis 3 or 4). The nerve-supply of the dorsal group is strictly branchiomeric; in the middle, and still more in the ventral group, this condition is not retained.

Between the two rami of the lower jaw is situated a muscle with transverse fibres (the *mylohyoid* or intermandibular muscle), supplied by the third division of the trigeminal and the facial nerve; this represents the last remnants of the ventral superficial constrictor muscle of Fishes. As elevator of the floor of the mouth, it stands in important relation to respiration and deglutition, and is retained throughout the rest of the Vertebrata up to Man (Figs. 140, 141).

A continuation of the trunk-musculature (the *omo-*, *sterno-*, and *genio-hyoid*), provided with tendinous intersections, lies above the mylohyoid (Fig. 141). These muscles, which serve to pull the visceral skeleton forwards and backwards, are supplied by the first and second spinal nerves.

In contrast to Fishes, there is in Amphibians a definite differentiation into muscles of the tongue, that is, into a *hyoglossus* and a *genioglossus;* these also must be considered as originating from the anterior end of the ventral muscles of the trunk; they are present in all Vertebrates from the Amphibia onwards, and are supplied by the hypoglossal—that is, the first (or second, Anura) spinal nerve.

In the Perennibranchiata and in Salamander larvæ the muscles of the hyoid and of the visceral arches may, by analogy with Fishes, be divided into a ventral and a dorsal group; the latter disappears in adult Salamanders and Anurans, only the ventral persisting. Their function is to raise and depress the branchial arches, as well as to draw them forwards and backwards. To these may be added, in branchiate forms, levators and adductors of the external gills (Figs. 140 and 141). They are innervated by the vagus and glossopharyngeal.

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[1] The visceral muscles of Polypterus are of especial interest, as they present an intermediate condition between those of Elasmobranchs and Urodeles.

The jaw-muscles may be divided into a depressor (*digastric*, or *biventer mandibulæ*, which here has only a single belly, Fig. 140), supplied by the facial nerve, and into several elevators of the lower jaw (*masseter*, *temporal*, and *pterygoid* muscles), supplied by the third division of the trigeminal. The last-mentioned muscles may be derived from the adductor of the mandible of Elasmobranchs, and the biventer from the portion of the superficial constrictor of Fishes which passes to the lower jaw: it arises from the same matrix as the platysma, and serves to open the mouth.

Amniota.—With the simplification of the visceral skeleton in Amniota there is a considerable reduction of the musculature belonging to it. All muscles connected with branchial respiration are of course wanting, and the ventral trunk-muscles, as mentioned above, are always interrupted in their forward extension by the sternum and pectoral arch. At the same time, the muscles along the neck and on the floor of the mouth met with in Amphibia are present here also; they are the mylo-, sterno-, omo-, and geniohyoid, as well as the hyoglossus and genioglossus. To these may be also added a sternothyroid, and a thyrohyoid continued forwards from it.

The stylohyoid, styloglossus, and stylopharyngeus of Mammals, arising from the styloid process and stylohyoid ligament and undergoing numerous variations, are peculiar to Mammals. They are supplied partly by the facial nerve, partly by the glossopharyngeal, and act as retractors of the tongue and levators of the pharynx and hyoid.[1]

The muscles of the jaws resemble those of Amphibia, although, especially in the case of the pterygoids, they are much more sharply differentiated into superficial and deep or external and internal portions, and may become subdivided secondarily (*e.g.* in the region of the temporal muscle): they are throughout more strongly developed.[2]

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[1] For the *tensor tympani* and *stapedius* muscles, cf. under Auditory Organ. The latter muscle, together with the stylohyoid, is possibly derived from the dorsal portion of the deep constrictor layer of Fishes which passes to the hyoid, but more probably corresponds to the ventral portion of this muscle.

[2] An anterior belly of the biventer appears in Mammals in consequence of a shifting of the superficial layer of the mylohyoid, the fibres of which are originally transverse. Its connection with the tendon of the posterior belly is therefore secondary, as are also the relations of the mylohyoid to the hyoid bone.

D. ELECTRIC ORGANS.

ELECTRIC organs are present in some Fishes, being most strongly developed in certain Rays (Torpedinidæ, *e.g.* *Torpedo*, *Hypnos*) found in the Atlantic Ocean and various southern seas, in a South American Eel (*Gymnotus electricus*) and in an African Siluroid (*Malopterurus electricus*). Gymnotus possesses by far the strongest electric power, next to it comes Malopterurus, and then Torpedo. The electric batteries of these three Fishes are situated in different parts of the body: in Torpedo they have the form of a broad mass, extending throughout the substance of that part of the body lying between the gill-sacs and the propterygium on either side of the head (Fig. 142); in Gymnotus they lie in the ventral region of the enormously long tail (Fig. 143), that is, in the position usually occupied by the ventral portion of the great lateral muscles; and finally, in Malopterurus, the electric organ extends between the skin and muscles round almost the entire circumference of the body, thus enclosing the Fish like a mantle: it is especially strongly developed along the sides, but is separated by the branchial apparatus into dorsal and ventral portions.

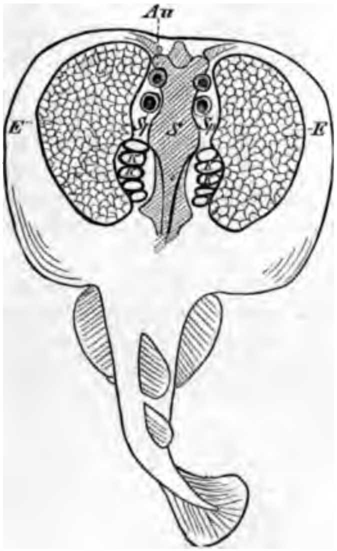

FIG. 142. — *Torpedo marmorata*, WITH THE ELECTRIC ORGANS (*E*) EXPOSED.

Au, eye; *KK*, gill clefts; *S*, skull; *Sp*, spiracle.

The electric power of those Fishes which were formerly known as "pseudo-electric" has now been fully demonstrated, though it is much feebler than in the forms described above. To this category belong, *e.g.* all the Rays, excluding Torpedo, and the various species of *Mormyrus* and *Gymnarchus* (both belonging to the Teleostei). In all these the electric organs lie on either side of the end of the tail and have a metameric arrangement like that of the caudal muscles; in the Mormyridæ, for example, there is on either side an upper and lower row of electric organs. In addition to the Fishes here referred to, electric organs have also been described in other Teleosts (*e.g. Astroscopus*).

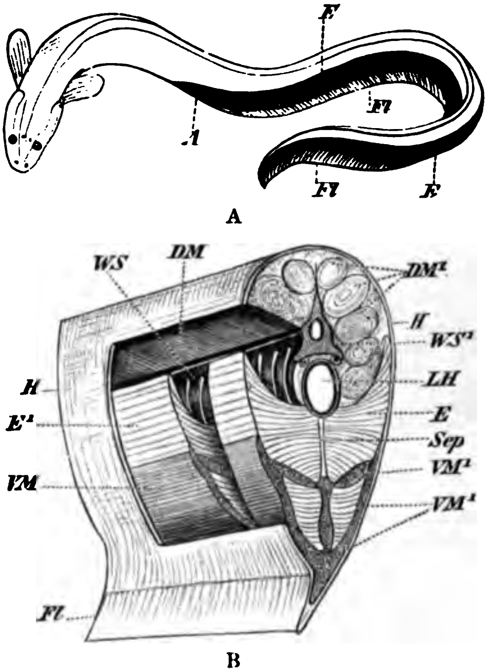

Fig. 143, A and B.—The Electric Organ of *Gymnotus electricus*. (B, from a preparation by A. Ecker.)

A, anus; *DM*, *DM*¹, dorsal portions of the great lateral muscles, seen partly in transverse, partly in longitudinal, section; *E*, the electric organ, seen in transverse section at *E* (B), and from the side at *E*¹; *Fl*, fin; *H*, skin; *LH*, posterior end of body-cavity; *Sep*, median longitudinal fibrous septum between the left and right electric organ and lateral trunk-muscles; *VM*, *VM*¹, ventral portions of the great lateral muscles, seen partly in transverse, partly in longitudinal, section; *WS*, vertebral column from the side, showing the spinal nerves, and *WS*¹, in transverse section.

With the possible exception of Malopterurus, in which the electric apparatus is said to be derived from the epiderm, the electric organs of Fishes consist of metamorphosed striated muscular fibres, and the nerve-endings belonging to them are the homologues of the motor end-plates which are ordinarily found on muscles.

As regards the structure of the electric organs, the same essential arrangements are met with in all. The framework is formed of fibrous tissue enclosing numerous cells, which, running partly longitudinally, partly transversely through the organ, gives rise to numerous polygonal or more or less rounded chambers or compartments. These latter are arranged in rows, either along the longitudinal axis of the body (Gymnotus, Malopterurus) or in a dorso-ventral direction (Torpedo), forming definite prismatic columns (Fig. 144). The compartments are filled with a homogeneous fluid or semi-fluid substance, the nature of which is not thoroughly understood. It is known to correspond to modified muscle-substance, and it contains numerous large, round and oval nuclei, as well as certain highly refracting bodies.

Numerous vessels and nerves ramify in the connective tissue lying between these compartments, the nerves being enclosed in thick sheaths, and having a great variety of origin according to the species of Fish under consideration. In Torpedo, in which the electric organs probably arise in connection with the great adductor muscle of the mandible and the constrictor of the gill-arches, the nerves arise from the "electric lobe" of the medulla oblongata, a single branch coming also from the trigeminal; in all "pseudo-electric" Fishes, as well as in Gymnotus, in which over two hundred nerves pass to the electric organ, they arise from the spinal cord, and most probably are in the closest relation with the ventral cornua, which are particularly well developed in the last-named Fish. It is remarkable that the electric nerves of Malopterurus arise on either side from a single enormous lens-shaped nerve-cell, which, situated in the neighbourhood of the second spinal nerve, is continued into a very large primitive-fibre, which passes towards the end of the tail, dividing as it goes. The latter is invested by a thick sheath.

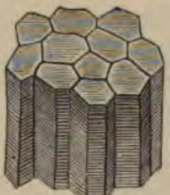

FIG. 144.—ELECTRIC PRISMS OF *Torpedo marmorata.* (Semi-diagrammatic.)

It is stated that in all electric Fishes the side of the electric plate on which the nerve branches out is negative at the moment of discharge, while the opposite side is positive. Thus the different arrangement of the parts in Gymnotus and Malopterurus renders it clear that the electric shock must pass in different directions in these Fishes: in Malopterurus it passes from the head to the tail, and in Gymnotus in the contrary direction, while in Torpedo the discharge passes from below upwards.

Experiments have shown that all electric Fishes are proof against the electric current, with the limitation that muscles and nerves—even the electric nerves themselves—separated out from the body are capable of being excited by the current. "The last and most important question with regard to the electric Fishes naturally concerns the mechanism whereby the electric plates become temporarily charged with electricity. The reply to this question, although probably not so difficult a one as that relating to the mechanism of muscular contraction, is still far from being answered" (Du Bois-Reymond). The only thing that can be stated with certainty is, that the electromotive force is under the control of the will.

E. NERVOUS SYSTEM.

The nervous system has the important function of placing the organism in communication with its surroundings, stimuli received by the sensory organs being transformed into nerve-impulses which are conducted along the *afferent* or *sensory nerve-tracks* to the central organ of the system. In the latter these stimuli are transformed, or new ones are originated, and they travel along the *efferent* or *motor nerve-tracks* to muscular elements, thus causing their contraction, or to glands, causing them to secrete. The intimate connection between muscle and nerve has already been referred to.

It was pointed out in the Introduction that the nervous system arises from the ectoderm. The parts of it which first become differentiated histologically are the **nerve-cells** (*ganglion-cells*), from which **nerve-fibres** arise later and serve as the conductors of nervous impulses. The most important constituent of the nerve-fibre is a central *neuraxis* or *axis-fibre*, and in those nerve-fibres which are spoken of as medullated this is surrounded by a highly refractile, fat-like substance (myelin), which forms the *medullary sheath*. In certain (non-medullated) nerve-fibres this sheath is wanting, but the two kinds of fibres are not sharply marked off from one another, either locally or genetically: a fibre may be medullated in one part of its course, and non-medullated in another. Externally each nerve-fibre is enclosed by a delicate sheath, the *neurilemma*.

Part of the ectodermic tissue which forms the nervous system of the embryo does not become transformed into nervous tissue, but gives rise to an epithelial layer (*ependyme*) and also to a supporting, connecting, or isolating framework—the *neuroglia*, which plays a very important part in the central nervous system; externally, investing membranes as well as blood- and lymph-vessels are formed from the mesoderm. As compared with the central organs, the peripheral tracks are comparatively poorly supplied with blood.

The nervous system thus consists of *central* and *peripheral* portions (Fig. 145). The central part (*brain* and *spinal cord*) is

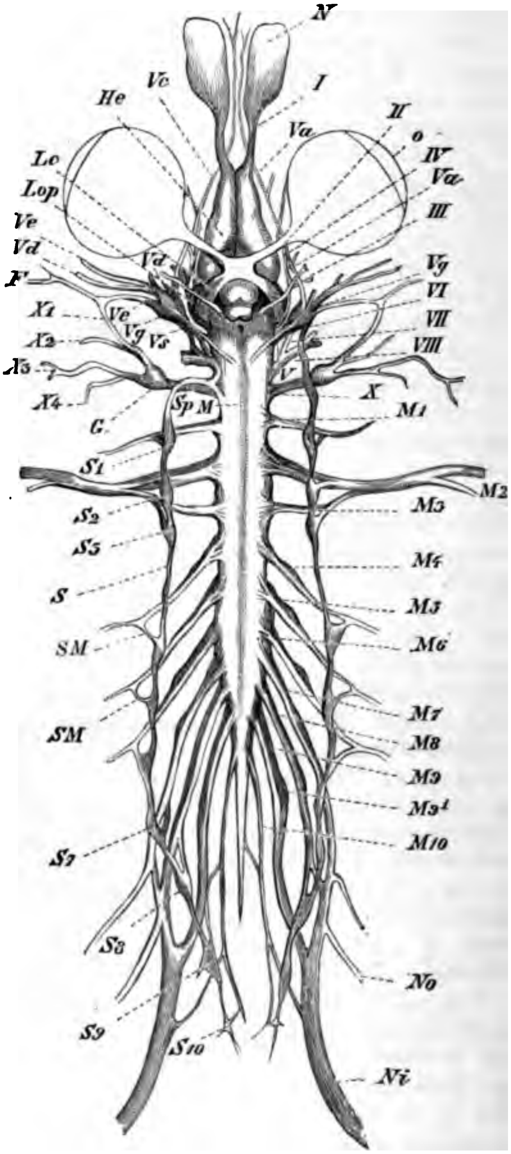

FIG. 145.—THE ENTIRE NERVOUS SYSTEM OF THE FROG. **(After A. Ecker.)** From the ventral side.

F, facial nerve ; *G*, ganglion of the vagus ; *He*, cerebral hemispheres ; ***I* to *X*, first to tenth cerebral nerves** ; *Lop*, optic lobes ; *M*, **spinal cord ; *M*1 to *M*10,** spinal nerves, which are connected at *SM* **by branches (rami communicantes)** with the ganglia (*S*1 to *S*10) of the sympathetic (*S*) ; ***N*, nasal sac ; *Ni*, sciatic** nerve ; *No*, femoral nerve ; *o*, eye ; *Va* to *Ve*, the **different branches of the trigeminal** ; *Vg*, Gasserian ganglion ; *Vs*, connection of the **sympathetic with the** Gasserian ganglion ; *X*1 to *X*4, the different branches of the **vagus. Some of the** *fibres* of the sympathetic should be shown **accompanying the vagus peripherally.**

the first to arise, and is formed as a direct product of the ectoderm; the peripheral portion (*cerebral*, *spinal*, and *sympathetic nerves*, and their ganglia) becomes established later.

1. THE CENTRAL NERVOUS SYSTEM.

The first indication of the central nervous system is a longitudinal furrow (*medullary groove*, Fig. 6, A) which appears on the dorsal side of the embryo, and which gradually becomes converted into a tube by the meeting of its edges; this tube, consisting originally of epithelial cells like the ectoderm from which it arises, then becomes separated from the latter, and gives rise to the hollow *medullary cord*[1] (Fig. 6, B), in which nerve-cells and fibres become differentiated; it comprises a more expanded anterior, and a longer and more slender posterior section. From the former arises the **brain**, from the latter the **spinal cord.**

In an early stage of development the lumen of the medullary cord is primitively continuous posteriorly with that of the primary intestine by the *neurenteric canal*, but this connection soon disappears. The cord consists of a cylindrical or more or less flattened tube, the cavity of which expands in front to form the *ventricles* of the brain, and is lined by ciliated epithelium. With the thickening of the walls of the tube, this cavity becomes greatly reduced, and in the spinal cord is spoken of as the *central canal.*

Some of the cells in the brain and spinal cord serve as sensory centres, others as motor-centres, new centres being added which complicate the originally simple reflex circuit, and various other modifications gradually occur in the course of development of the head.

Membranes of the brain and spinal cord (*meninges*).

In Amphioxus, the central nervous system is enclosed by an undifferentiated investment of connective tissue. In the lowest Craniata, a differentiation takes place into a *primitive meninx*, which closely invests the spinal cord, and a second membrane (*endorachis*), which lines the vertebral canal: the latter, formerly known as the "dura vertebralis," is comparable merely to the perichondrium or periosteum, and has nothing to do with the meninges proper. The blood-vessels supplying the spinal cord are contained in the primitive meninx, the space and tissue directly external to which may be spoken of as the *perimeningeal space* and *tissue*. This condition is retained in Fishes (Fig. 146, A).

A further process of differentiation takes place in Urodeles and is more marked in Anurans, reaching a higher stage in Reptiles and a still higher one in Birds. This process consists in the appearance of a lymph-space in the primitive meningeal membrane, dividing it into an outer *dura mater spinalis* and an inner *primitive pia mater*. There is thus a *peridural* or *epidural space* external to the dura, and a *subdural space* between it and the primitive pia (B).

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[1] The cord is at first solid in certain Fishes (*e.g.* Petromyzon, Lepidosteus, Amia, Teleostei, Lepidosiren), its cavity appearing later.

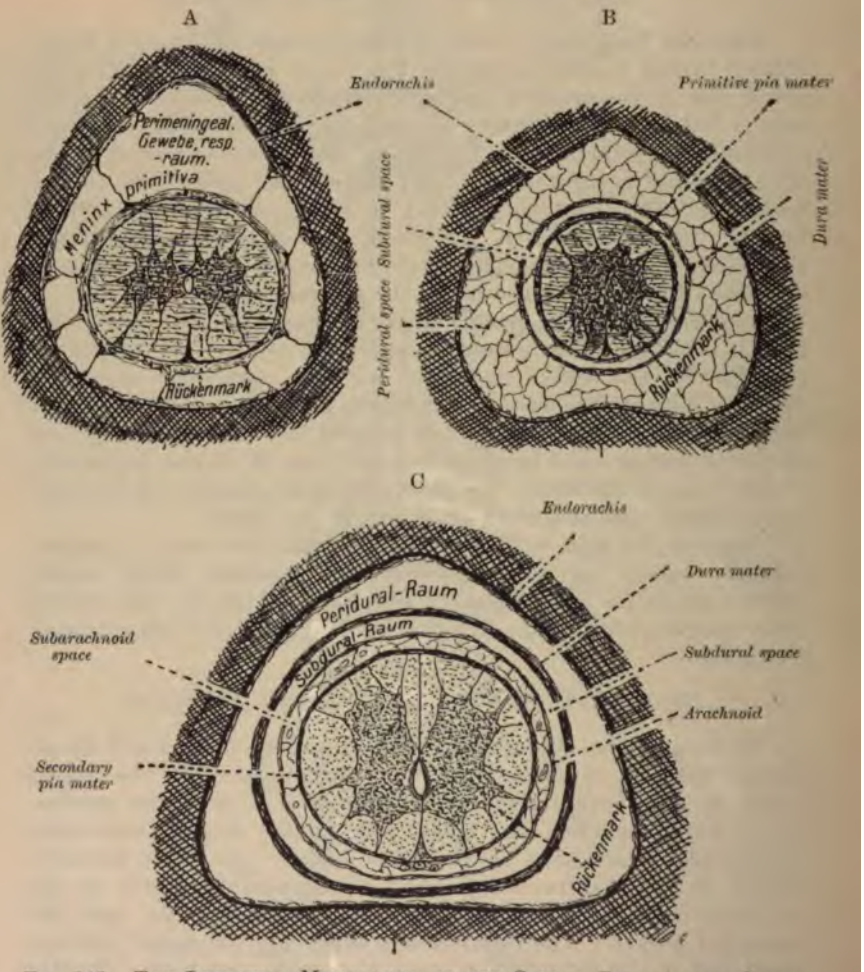

FIG. 146.—THE INVESTING MEMBRANES OF THE SPINAL CORD IN THE CHIEF VERTEBRATE GROUPS. A, Fishes; B, Amphibia and Sauropsida; C, Mammalia. Semidiagrammatic. (After Sterzi.) *Rückenmark*, spinal cord.

In Mammals, the pia is considerably thicker, and the lymph spaces which it encloses are more marked: it becomes separated into two layers, the inner of which gives rise to the vascular *secondary* or *definitive pia*, and the outer to the *arachnoid*.

In consequence of this process of differentiation, the originally single perimedullary space is now represented by three lymph spaces:—a *peridural*, a *subdural*, and a *subarachnoid space* (C). The last mentioned encloses a network of trabeculæ.[1]

The brain-membranes are formed in essentially the same way as those of the spinal cord. The dura mater, however, possibly owing to the rapid growth of the brain, becomes pressed against the periosteum (so-called "*endocranium*," corresponding to the endorachis of the spinal column), with which it may become fused (*e.g.* Mammals) and thus was formerly known as the outer layer of the dura.[2]

In Fishes and tailed Amphibians, the whole subdural space is filled by a loose tissue consisting of meshes enclosing lymphoid and fatty tissue, while in Anurans this is only the case in the anterior part of the skull. Further back, to the end of the spinal canal, there is a definite continuous space filled with lymph, and this is especially well developed on the dorsal side of the brain and spinal cord.

Functionally, the dura serves as a kind of internal periosteum, while the vascular pia is important in connection with the nutrition of the central nervous system. In places where the walls of the brain are epithelial, and do not become converted into nervous tissue, the pia also takes part secondarily in lining the ventricles, into which it may extend, pushing the epithelial wall (ependyme) before it, and thus giving rise to *telæ* or *plexus choroidei*, which are very important throughout the Vertebrate series.[3]

The arachnoid, which, as mentioned above, becomes differentiated between the dura and pia, is not really a membrane: it consists of an extensive system of meshes of lymphoid (adenoid) tissue, the cavities in which are lined by an epithelium and contain a serous or lymphoid fluid. The meshes bridge over all involutions and irregularities of the surface of the brain, and form a delicate external lamella separating them from the subdural space all along the cerebro-spinal canal.

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[1] The cause of this gradual increase in complication is to be traced in the first instance to the increasing vascularisation of the spinal cord in passing from the lower to the higher Vertebrates: this results in an increase in the quantity of lymph and necessitates an arrangement of larger channels for carrying it off.

[2] The morphological difference between these two membranes is seen most plainly at the optic foramen, at which the periosteum of the cranium is directly continuous with that of the orbit, while the dura proper forms the sheath of the optic nerve. The mode of origin of the so-called *sinus duræ matris* is not known with certainty, but they appear to have nothing to do with the dura proper and to correspond to sinuous enlargements of the periosteal "endocranium," as is indicated by similar spaces in the endorachis of Anamnia, Reptiles, and mammalian embryos, which are especially well seen around parts of the brain in Urodeles. In Anurans they even extend beyond the cranial cavity along the whole length of the spinal canal. (Cf. under Auditory Organ—perilymphatic and endolymphatic ducts.)

[3] The brain-membranes in Sauropsida require further investigation. In Mammals the dura gives rise to folds extending between parts of the brain, known as the *falx* and the *tentorium*. The former, slight indications of which are also seen in Birds, extends between the two hemispheres, the latter between the hind-brain and the occipital lobes of the hemispheres: both may become ossified (*e.g.* in Carnivora).

In all Vertebrates the subarachnoid space communicates in the region of the hind-brain (medulla oblongata) with the ventricles and central canal, so that there is a free passage into these for the albuminous cerebro-spinal or arachnoid fluid, which is mainly formed in connection with the ependyme cells covering the choroid plexuses in the ventricles.

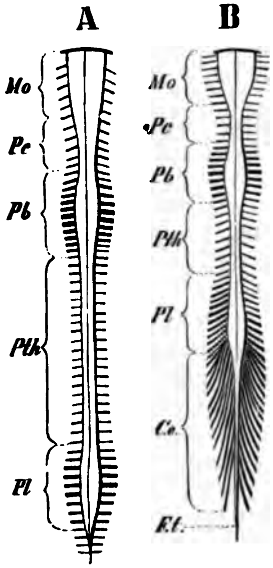

FIG. 147.—DIAGRAMS OF THE SPINAL CORD AND ITS NERVES. In A the cord passes to the end of the tail, and at B it ends more anteriorly and passes behind into a longer filum terminale.

Ce, cauda equina; *F.t*, filum terminale; *M.o*, medulla oblongata; *Pb*, brachial plexus; *Pc*, cervical nerves; *Pl*, lumbo-sacral plexus; *P.th*, thoracic nerves.

1. The Spinal Cord.

The spinal cord is at first of a uniform diameter throughout, but later, when a richer nerve-supply becomes needed for the extremities, it exhibits in these regions definite swellings—the *brachial* and *lumbo-sacral* enlargements (Fig. 147). The cord originally extends along the whole length of the neural canal, but its growth is usually less rapid than that of the vertebral axis, so that it is eventually considerably shorter than the latter. In such cases (*e.g.* Primates, Cheiroptera, Insectivora, Anura—Figs. 145 and 147) it passes at its posterior end into a brush-like mass of nerves, the so-called *cauda equina*; these lie within the neural canal, and the sacral nerves arise from them. An axial prolongation of the spinal cord nevertheless extends far back, but is reduced to a thin thread-like *filum terminale*.

The bilaterally-symmetrical form of the spinal cord is pronounced by the presence of a longitudinal fissure extending along it ventrally; this *ventral fissure* is not always present, and the so-called "*dorsal fissure*," which is formed by obliteration of the greater part of the primitive central canal, is due to the presence of a septum formed from connecting substance, the ependyme.[1] If one imagines the points of exit of the dorsal (sensory) and ventral (motor) nerve-roots to be respectively connected together by a longitudinal line, each half of the spinal cord would thus be divided into three columns,—a ventral, lateral, and dorsal. Anteriorly the cord becomes continuous with the posterior portion of the brain (medulla oblongata), with the ventricle of which the central canal communicates.

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[1] A secondary ventricle-like enlargement of the posterior end of the central canal in many Mammals and other Vertebrates must not be confused with the so-called *sinus rhomboidalis* in the lumbar region of the cord in Birds, which arises by a separation of the lateral halves of the cord and is filled with modified *neuroglia*, thus forming a much thickened dorsal septum.

As regards its minute structure, two kinds of nervous tissue can be distinguished in the spinal cord,—a *white substance*, consisting of nerve-fibres only, and a *gray substance*, composed of nerve-cells as well as fibres.[1] Their relative positions vary in the various vertebrate groups, as well as in different regions of the cord; the white substance, however, has in general a more peripheral, the gray a more central position, the latter usually presenting a pair of *dorsal* and *ventral cornua* in transverse section, its groups of cells showing in many places a metameric arrangement.[2]

2. The Brain.

Before the medullary groove becomes closed, three swellings may be seen at the anterior enlarged part of the medullary tube: these are spoken of as the primary *anterior*, *middle*, and *posterior cerebral vesicles*, or *fore-*, *mid-*, and *hind-brain*. (Fig. 148). The cavities of the vesicles are in direct connection with the central canal of the spinal cord.

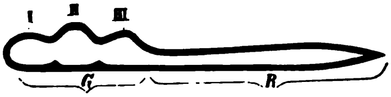

FIG. 148.—DIAGRAM OF THE EMBRYONIC CONDITION OF THE CENTRAL NERVOUS SYSTEM.

G, brain, with its three primary vesicles, *I*, *II*, *III*; *R*, spinal cord.

A differentiation of the primary fore-brain and hind-brain respectively into two parts then takes place, and thus *five* divisions of the brain may be distinguished. Counted from before backwards these are the *telencephalon* (secondary fore-brain or cerebral rudiment), *diencephalon* (primary fore-brain or twixt-brain), *mesencephalon* (mid-brain), *metencephalon* (secondary hind-brain), and

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[1] Peculiar structures, known as Reissner's fibres, arising in the brain and extending along the spinal cord, occur in all vertebrate Classes. They represent an ancient but highly differentiated apparatus, the function of which is to pass optic stimuli by reflex action to the motor tracks of the cord. These fibres are largest in Elasmobranchs and Teleosts, and are reduced or wanting in blind animals and those in which the eyes have undergone reduction.

[2] In Struthious Birds a row of elevations occurs in the lumbo-sacral region, recalling the metameric segmentation of the cord in the Teleost *Trigla*. The originally metameric character of the cord is also indicated phylogenetically and ontogenetically by the primary, segmental blood-vessels. The dorsal and ventral longitudinal vascular trunks arise secondarily.

myelencephalon[1] (primary hind-brain). The telencephalon usually gives rise to a pair of lobes, the *cerebral hemispheres*, and the mid-brain to a pair of *optic lobes* or *corpora bigemina* dorsally, and to two longitudinal bands, the *crura cerebri*, ventrally. The metencephalon is also spoken of as the *cerebellum*, and the myelencephalon as the *bulb* or *medulla oblongata*. From the secondary fore-brain paired *olfactory lobes*[2] are given off anteriorly, and its floor or basal portion becomes thickened to form a large "basal ganglion," the *corpus striatum*, while its peripheral part is distinguished as the "mantle" or *pallium* (Fig 149).[3]

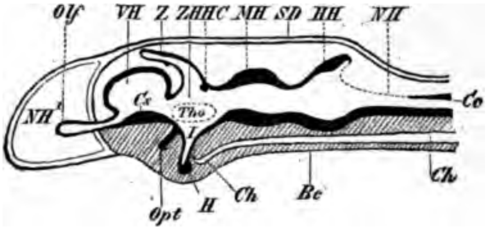

FIG. 149.—LONGITUDINAL SECTION THROUGH THE SKULL AND BRAIN OF AN (IDEAL) VERTEBRATE EMBRYO. (In part after Huxley.)

Bc, basis cranii; *Cc*, central canal of spinal cord; *Ch*, notochord; *HC*, posterior commissure; *HH*, cerebellum (metencephalon, secondary hind-brain); *MH*, mid-brain (mesencephalon); *NH*, primary hind-brain (myelencephalon); *NH'*, nasal cavity; *SD*, roof of skull; *VH*, secondary fore-brain (telencephalon), showing the corpus striatum (*Cs*) at the base, and the olfactory lobe (*Olf*) anteriorly; *ZH*, diencephalon (primary fore-brain), which has given rise dorsally to the pineal body (epiphysis, *Z*), and ventrally to the infundibulum (*I*), to which the pituitary body (hypophysis, *H*) is attached: anteriorly to this is seen the optic nerve (*Opt*), arising from the optic thalamus (*Tho*).

The pallial region undergoes an important process of development in passing upwards from lower to higher forms, gradually becoming differentiated histologically into a layer of *cortical gray matter* of great physiological importance, the relative differentiation of which stands in close relation to the mental development of the animal. The telencephalon reaches its greatest perfection in Mammals, more especially in Man, while in certain lower Vertebrates the cortex is partially or entirely non-nervous and retains its embryonic epithelial character: this is usually regarded as being due to regressive metamorphosis, the cause of which, however, is difficult to explain. The relative distribution of the gray and white matter differs in various parts of the brain.

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[1] There is still a want of unanimity in the use of this nomenclature, and many of the terms given above, as well as others with a similar ending, are used in different senses by different morphologists.

[2] The olfactory lobes are of great importance phylogenetically, as the origin of the telencephalon, and more especially of its deeper basal portion, is closely connected with the olfactory organ.

[3] From the primarily epithelial pallium arises a median dorsal outgrowth, the *paraphysis* (Fig. 150), just anteriorly to a transverse fold of the epithelial roof (*velum transversum*) which separates the ventricles of the primary and secondary fore-brain, and on the edge of which a posterior pallial commissure can be recognised (*e.g.* in Lizards): this fold encloses a vascular thickening of the pia mater (*choroid plexus*), from which the paraphysis is not always distinguishable (cf. Fig. 165). The latter apparently represents a glandular organ, recalling that connected with the infundibulum: whether it also includes the vestige of a sensory *apparatus, like* the parietal and pineal organs, is doubtful (cf. pp. 202 and 203).

Connecting the two lateral halves of the brain are certain transverse bands of nerve-fibres or *commissures.* In addition to a small *superior* or *habenular commissure* in the pallium (Fig. 150), an *anterior commissure* is present in the posterior region of the secondary fore-brain, a *middle* in the primary fore-brain (in Mammals only), and a *posterior* in the anterior part of the mid-brain. In addition to these, others may be developed in the pallial region (*e.g. anterior* and *posterior pallial* commissures, cf. Fig. 165); and amongst Mammals those known as the *corpus callosum* and *fornix* are of great importance.

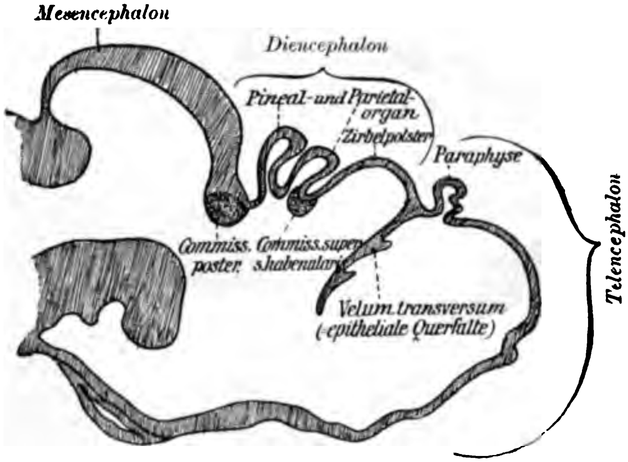
Mesencephalon
Diencephalon
Pineal- and Parietal-organ
Zirbelpolster
Paraphyse
Telencephalon
Commiss. poster.
Commiss. super. s. habenularis
Velum transversum (-epitheliale Querfalte)

FIG. 150.—DIAGRAMMATIC LONGITUDINAL SECTION THROUGH PART OF THE EMBRYONIC BRAIN.

Zirbelpolster, pineal cushion.

The outer surface of the hemispheres is more or less smooth, except amongst the Mammalia, in which fissures (*sulci*) and convolutions (*gyri*) may be present. These consist of folds of the entire pallium or cortex, and they cause a greater or less increase of the superficial area.

From the primary fore-brain, the ventricle of which is walled in anteriorly by the *lamina terminalis*, the following structures also arise (Fig. 149):—the *optic thalami*, formed as thickenings of its basal walls, and the *ganglia habenulæ* on the posterior lateral margin of the dorsal region, with the *superior commissure* between them; the primary *optic vesicles*, arising as paired ventro-lateral outgrowths, from which the *optic nerves* and *retina* with its pigment epithelium are derived later; the *pineal apparatus*, developed as outgrowths of the roof; and finally, the *infundibulum*, formed as an extension of the floor, together with part of the *pituitary body* (*hypophysis*). Another portion of the pituitary body is derived from the epithelium of the primary oral involution (stomodæum).[1]

The *pineal apparatus* consists of the *epiphysis* or *pineal organ proper*, which persists in a more or less vestigial condition in all Vertebrates, and of a more anterior outgrowth which may be called the *parietal organ*, arising from the epiphysis or independently from the roof of the diencephalon, and becoming atrophied in the majority of Vertebrates. Each of these structures represents a vestigial sensory organ, and may retain to a greater or less extent the characters of a *median eye*, which in some cases has probably a light-perceiving function. Certain facts indicate that these organs may have been paired primitively or that the two correspond to members of a pair; but further researches are desirable on this point, as well as on the relation of the two organs

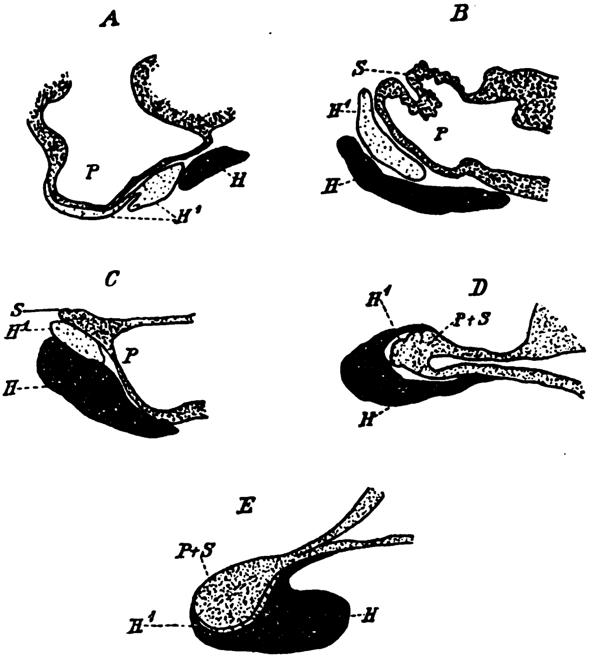

Fig. 151.—Diagram illustrating the Structure of the Hypophysis of Vertebrates. *A*, Petromyzon; *B*, Pisces; *C*, Amphibia; *D*, Sauropsida; *E*, Mammalia. (After Sterzi.)

H, "chromophilous" portion, and H^1, "chromophobic" portion of hypophysis; *P*, infundibular process; *S*, saccus vasculosus.

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[1] Possibly the endodermic epithelium of the primary fore-gut may also take part in its formation.

to one another and the nature of certain accessory vesicles in this region found in certain forms (*e.g.* Anguis). Both pineal and parietal organs are in the embryo connected with the brain by a special nerve or tract which grows out from the organ and becomes connected with the brain secondarily (cf. Figs. 165 and 168).

As already stated, a nervous and an epithelial portion are to be distinguished in the hypophysis, the former originating from the infundibulum, the latter from the epithelium of the stomodæum (Fig. 151). In Cyclostomes the nervous portion consists of a thin-walled sac arising from the infundibulum (infundibular sac or process), which in all the true Fishes is in part thrown into folds by the invasion of numerous vessels. Thus arises the so-called *saccus vasculosus*, the development of which shows great variation amongst the different groups of Fishes. In the higher Vertebrates the infundibular process undergoes various modifications, especially as regards the saccus vasculosus,[1] only traces of which may still be recognisable (*e.g.* Mammals).

Both the primary and the secondary fore-brain are situated in the prechordal region of the skull, all the other divisions of the brain lying in its chordal portion (p. 75). The mid-brain and medulla oblongata undergo fewer modifications than the fore-brain, though each optic lobe becomes subdivided into an anterior and a posterior lobe in Mammals; only the anterior part of the thin roof of the medulla (*valve of Vieussens*) is nervous, while its floor becomes greatly thickened, and in Mammals gives rise anteriorly to a transverse band of fibres (*pons Varolii*). It is important to note that the greater number of the cerebral nerves arise from the medulla oblongata. The cerebellum may be more or less distinctly folded and subdivided into median and lateral lobes.

In the course of further development, the walls of the cerebral vesicles become more and more thickened, so that their cavities, transformed into the *ventricles* of the brain, undergo a gradual reduction (Fig. 152).

A series of unpaired ventricles (*telocœle, diacœle, mesocœle, metacœle*, and *myelocœle*) lying in the longitudinal axis of the brain, as well as paired ventricles, can be distinguished. When cerebral hemispheres are more or less distinctly developed, the telocœle gives rise to paired cavities extending into them and known as the *lateral ventricles* (= ventricles 1 and 2); each of these communicates with the diacœle or *third ventricle* (which extends into the infundibulum) by means of an opening, the *foramen of Monro*, and may be continued into the corresponding olfactory lobe as an *olfactory ventricle* or *rhinocœle*. Each optic lobe also usually contains an *optic ventricle*, or *optocœle*, communicating with the mesocœle (*iter* or *aqueduct of Sylvius*). There may be a distinct metacœle in the cerebellum opening into the myelocœle or *fourth ventricle*.[1]

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[1] Various hypotheses have been put forward with regard to the primary nature of the hypophysis: it may represent a sensory organ, or may correspond to the primitive mouth ("palæostoma") of the Protovertebrata, which is to a greater or less extent represented by the combined unpaired nasal and pituitary passage of Cyclostomes (see under Olfactory Organ, and Fig. 190): on the latter hypothesis the mouth of existing Vertebrates is a "neostoma." It is very probable, especially in the higher Vertebrates, that the epithelial part of the hypophysis has an important function as a ductless gland, which gives off its secretion into neighbouring blood- and lymph-capillaries.

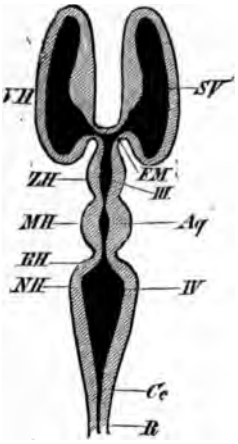

FIG. 152.—DIAGRAM OF THE VENTRICLES OF THE VERTEBRATE BRAIN.

Cc, central canal of the spinal cord (*R*); *HH*, cerebellum; *MH*, midbrain, which encloses the iter (*Aq*), communicating between the third and fourth ventricles; *NH*, medulla oblongata, with the fourth ventricle (*IV*); *VH*, cerebral hemispheres, with the lateral ventricles (*SV*); *ZH*, diencephalon, with the third ventricle (*III*); each lateral ventricle communicates with the third ventricle by a small aperture, the foramen of Monro (*FM*).

All five cerebral vesicles lie at first in the same horizontal plane, but in the course of development a *cerebral flexure* takes place, the axis of the vesicles becoming bent downwards, so that at a certain stage the mesencephalon forms the apparent apex of the brain. In Mammals, the parts of the brain become still further folded on one another, so that a parietal, a Varolian, and a cervical bend may be distinguished (Fig. 153): this process is connected with the further development of the skull and the rapid longitudinal growth of the brain.

In Fishes and Amphibians the cerebral flexure later becomes practically obliterated, but it persists more or less markedly in the higher types, more particularly in Mammals. In the latter Class, moreover, the original relation of the parts becomes still further complicated by the large development of the cerebral hemispheres, which grow backwards, and thus gradually overlie all the other parts of the brain: this condition of things attains its greatest perfection in Man.

Amphioxus.—The conical and enlarged anterior end of the spinal cord of the Lancelet contains a widened portion of the central canal which must be looked upon as a ventricle. This opens freely to the exterior dorsally by a *neuropore*, which represents the last indication of the primitive connection of the central nervous system with the outer skin. It is impossible to say with any degree of certainty to what extent this " brain " of Amphioxus corresponds to parts of the Craniate brain.

Cyclostomes.—The brain of these forms remains in many respects in an embryonic condition: a dorsal connection of its two halves by nervous elements is very incomplete, narrow bridges of nervous substance only occurring in the primitive hind-brain, the posterior portion of the mid-brain, the posterior commissure, and the ganglion habenulæ of the right side. The main part of the roof consists of membrane and vessels.

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[1] A so-called "fifth" ventricle, lying between the corpus callosum and fornix, is found in Mammals, but morphologically it has nothing to do with the ventricles proper, and simply represents a space between the thin internal walls (*septum lucidum*) of the two hemispheres.

In the larval Petromyzon or Ammocœte, very primitive conditions are met with (Fig. 154), and, as is also the case in the adult, the individual vesicles lie in an almost horizontal direction one behind the other; the telencephalon consists of a median part and of small paired hemispheres continuous anteriorly with the larger, rounded olfactory lobes. The median portion of the telocœle is continued transversely outwards into each hemisphere, in which it gives rise to a lateral ventricle: this is continued forwards for a short distance into the base of the olfactory lobe, as well as backwards into the hemisphere. The roof (pallium) of the median portion of the ventricle is non-nervous, and consists of a single layer of epithelial cells, which, together with the pia mater, has been removed in the preparation represented in Fig. 154, A. The mid-brain and elongated medulla oblongata are relatively broad, and the cerebellum is represented by a mere narrow ledge overhanging the fourth ventricle anteriorly. The roof of the mesocœle is formed mainly by a layer of epithelial cells, and, like that of the third and fourth ventricles, is covered by a thickened and vascular portion of the pia mater, or *choroid plexus*.

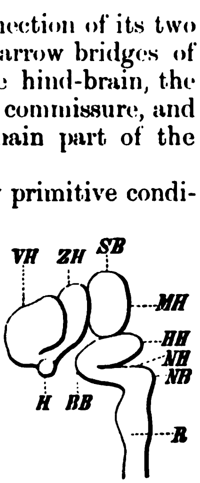

FIG. 153.—DIAGRAM TO ILLUSTRATE THE CEREBRAL FLEXURE OF A MAMMAL.

HH, metencephalon; *MH*, mesencephalon, which at *SB* forms the most projecting portion of the brain, representing the so-called "parietal bend"; *NH*, myelencephalon, forming the "cervical bend" (*NB*): the "Varolian bend" (*BB*) arises on the ventral circumference, at the junction between *HH* and *NH*; *R*, spinal cord; *VH*, telencephalon; *ZH*, diencephalon, with the pituitary body (*H*) at its base.

The brain of Myxinoids (Fig. 155) shows many peculiarities, and the morphology of its parts requires further investigation. Its subdivisions are broader and more closely approximated than in the Lamprey, and its right and left halves are more plainly marked off from one another by a continuous longitudinal dorsal furrow. No pallium is recognisable, at any rate in the adult. The ventricles have undergone reduction, and present individual variations: in the ventral region of the fore-brain there is a small isolated cavity which probably represents the vestige of a third ventricle. The broad olfactory lobes are separated from the telencephalon by a transverse furrow. The diencephalon is not visible from the dorsal side, but ventrally there is a distinct infundibular process. The mid-brain is the most prominent division: the mesocœle ends

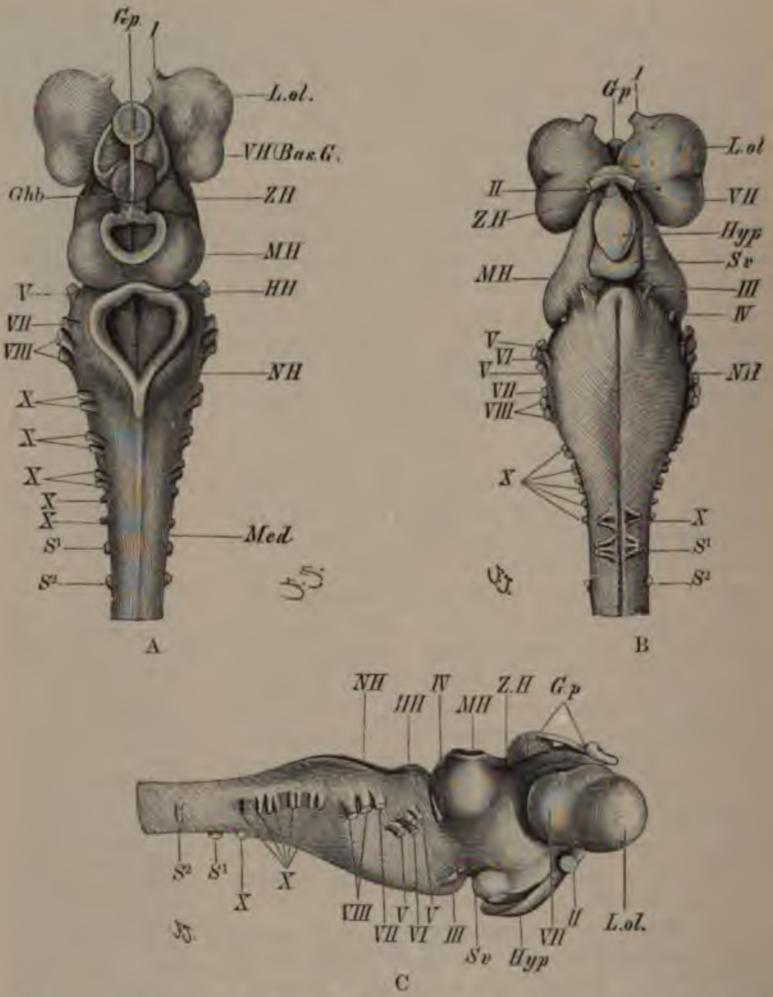

FIG. 154.—BRAIN OF LARVAL LAMPREY. A, from above; B, from below; C, from the side.

Ghb, ganglion habenulæ; *Gp*, pineal organ; *HH*, cerebellum; *Hyp*, hypophysis; *L.ol*, olfactory lobe; *Med*, spinal cord; *MH*, mid-brain; *NH*, medulla oblongata; S^1, S^2, first and second spinal nerves; *Sv*, saccus vasculosus; *VH* (*Bas.G*), cerebral hemispheres between which, in A, the median portion of the telencephalon is seen, with the pallium removed; *ZH*, diencephalon; *I-X*, cerebral nerves.

blindly in it anteriorly. The cerebellum is relatively much larger than in the Lamprey, and projects posteriorly so as to cover the fourth ventricle completely: it resembles that in certain embryonic

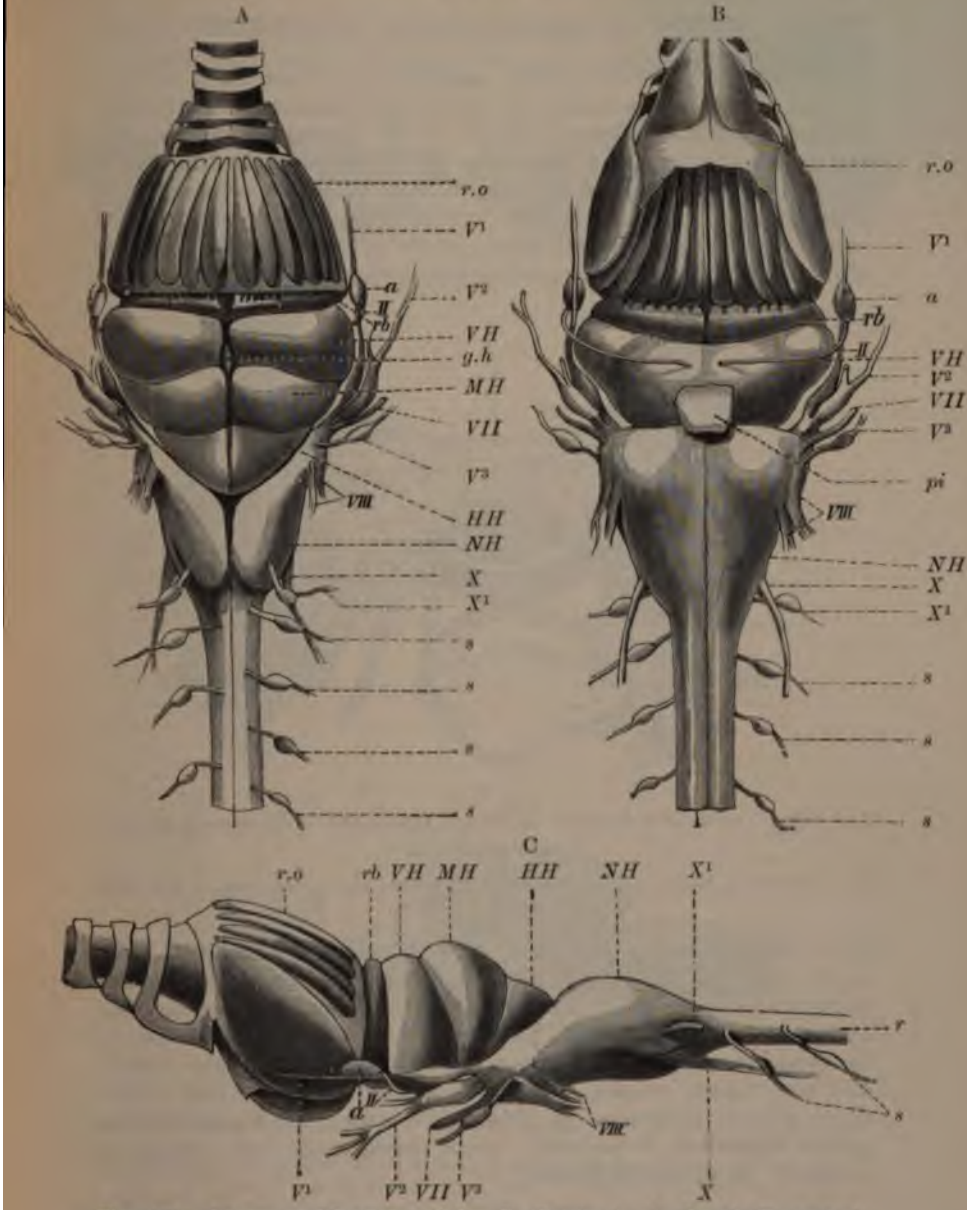

FIG. 155.—BRAIN OF MYXINE. (After G. Retzius.) A, dorsal; B, ventral; C, lateral view. The olfactory organ and its cartilaginous skeleton (*r.o*) is left *in situ*.

a, eye; *g.h*, ganglion habenulæ; *HH*, cerebellum; *II*, vestigial optic nerve; *MH*, mid-brain; *NH*, medulla oblongata; *pi*, infundibular process; *r*, spinal cord; *rb*, olfactory lobe; *s*, spinal nerves (dorsal roots and ganglia); $V^{1,2,3}$, trigeminal; *VH*, telencephalon; *VII*, facial; *VIII*, auditory; *X*, vagus; X^1, sensory branch of vagus or dorsal branch of a spino-occipital *nerve*.

stages of Teleosts. A large, paired, dorsal lobe is present on the medulla.[1]

In Petromyzon the pineal apparatus is represented by two vesicles, which are probably the displaced members of a pair, each connected with the dorsal surface of the diencephalon (ganglion habenulæ) and lying one above the other just beneath the roof of the skull ; the integument immediately above these vesicles is pigmentless. The cells on the ventral side of the larger dorsal vesicle (*epiphysis* or *pineal organ*—probably representing the organ of the right side) are arranged radially and contain pigment, forming a kind of retina, but they show signs of degeneration ; the lower vesicle or *parapineal* (left) *organ*, which probably corresponds to the parietal organ of Lizards (*q.v.*) is simpler and more variable, and is without pigment. The pineal stalk, arising just in front of the posterior commissure, passes directly into the dorsal vesicle, and the ventral vesicle is also connected with the roof of the diencephalon (habenular ganglion) by a stalk. In Myxinoids the pineal apparatus is evidently much degenerated, and nothing is known of an epiphysis proper.[2]

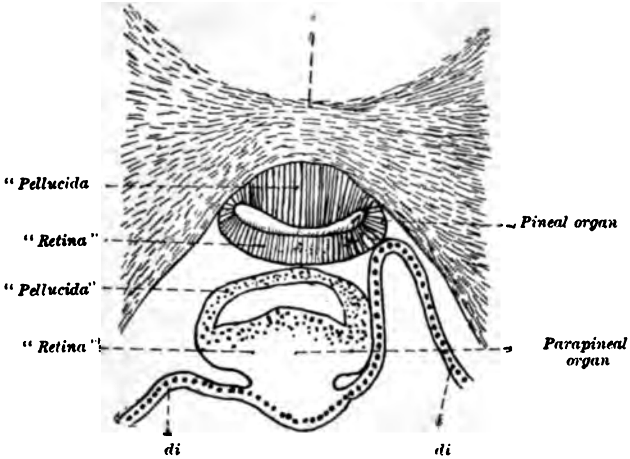

FIG. 156.—TRANSVERSE SECTION OF PINEAL APPARATUS OF *Petromyzon marinus*. (After Studnička.)

The connective tissue roof of the skull (*s*) is seen above, the roof of the third ventricle (*di*) below.

Elasmobranchs.—The brain of these Fishes, like that of Cyclostomes, is in many respects of a specialised form, characteristic of, and confined to, the group, though the particular regions are much more highly developed than in Cyclostomes: the pallium

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[1] The homology of the parts as given above has recently been questioned : it is possible that the division described as the telencephalon corresponds to the diencephalon, and that the "cerebellum" belongs to the mid-brain.

[2] For the hypophysis of Cyclostomes, see under Olfactory Organ.

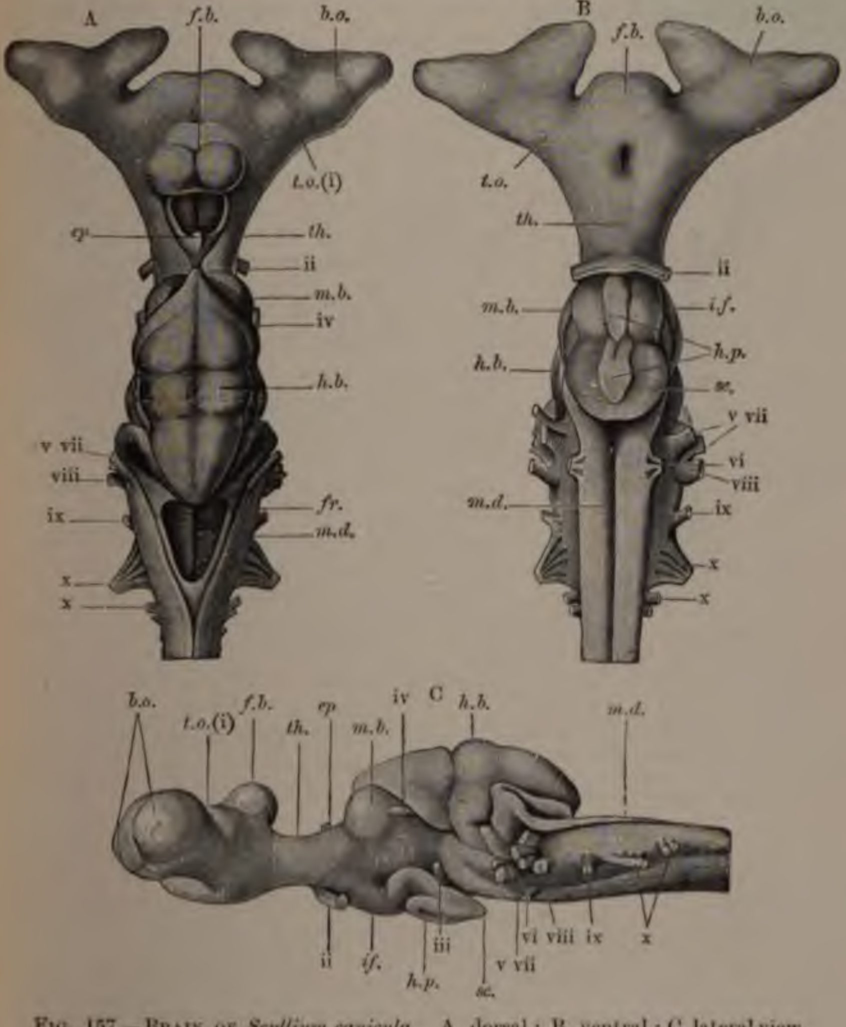

FIG. 157.—BRAIN OF *Scyllium canicula*. A, dorsal; B, ventral; C, lateral view.

b.o, olfactory bulb; *ep*, base of epiphysis; *f.b*, telencephalon; *fr*, fourth ventricle; *h.b*, cerebellum; *h.p*, hypophysis; *if*, lobi inferiores; *m.b*, mid-brain (optic lobes); *m.d*, medulla oblongata; *sc*, saccus vasculosus; *th*, diencephalon; *t.o*, olfactory tract (very short in Scyllium). The epithelial and vascular roof of the third and of the fourth ventricle has been removed. *ii-x*, cerebral nerves (the ventral vagus roots are omitted in B).

is almost exclusively nervous. According to its external form, two main types can be distinguished. Thus in Spinax, Scymnus, Notidanus, and the Holocephali, it is very narrow and elongated, while in the rest of the Plagiostomi the individual parts are more closely compressed and approximated together (Fig. 157). In almost all Sharks the telencephalon is relatively much larger than any of the other parts. The olfactory lobes arise from the anterior or antero-lateral ends of the telencephalon, and in some Elasmobranchs remain in close connection with it: in others, in which the olfactory capsules are situated further forwards, they become drawn out into long *olfactory tracts*, each arising from a basal *olfactory tubercle* and continuous anteriorly with an *olfactory bulb* from which the olfactory nerves arise.

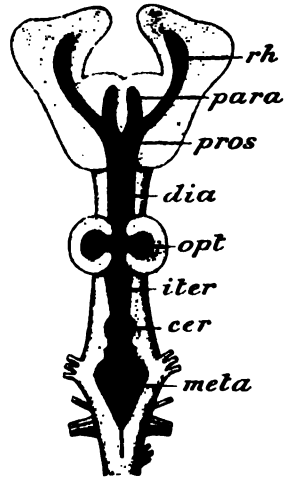

Fig. 158.—Brain of *Cheiloscyllium*. (From Parker and Haswell's *Zoology*.)

Viewed from the dorsal side, and the roofs of the various ventricles removed so as to show the relations of the cavities (semi-diagrammatic).

cer, dilatation from which the metacœle is given off; *dia*, diacœle—the reference line points to the opening leading into the infundibulum; *iter*, iter (mesocœle), into which the optocœles (*opt*) open; *meta*, myelocœle; *para*, lateral ventricle; *pros*, median part of telocœle; *rh*, rhinocœle.

A division of the telencephalon into paired halves is hardly indicated at all in Rays, and only slightly so in the commoner Dogfishes (*e.g.* Scyllium, Acanthias), in which, however, lateral and olfactory ventricles are present (Fig. 158). Only in Scymnus, and to some extent in the Notidanidæ, is there a distinct separation of the pallium into two hemispheres. In Rays there is only a small unpaired telocœle, the telencephalon consisting of a practically solid mass, and the olfactory lobes are also solid; in the Myliobatidæ there is no trace at all of a telocœle.

The narrow diencephalon is roofed over by a choroid plexus, and the tube-like epiphysis (wanting in Torpedo) may reach such a length as to extend beyond the anterior end of the brain for a considerable distance, and pass distally into or beyond the roof of the skull: no indication can be seen of a parietal organ. A pair of small lobes—the *lobi inferiores*—are present on the infundibulum, and a *saccus vasculosus* or infundibular gland, surrounded by a blood sinus, is present on the sides and floor of the infundibulum, with the ventricle in which it communicates and with which a pituitary body is connected posteriorly.

The cerebellum is always very large, overlapping the optic lobes and medulla oblongata to a greater or less extent: it is divided into several lobes lying one behind the other, and usually contains a metacœle opening into the fourth ventricle.

In Sharks, especially in Scymnus and the Notidanidæ, the medulla oblongata is elongated and cylindrical, while in Rays it is more compressed and triangular; at its anterior end are a number of elevations corresponding to origins of the nerves arising from the gray matter of the floor of the fourth ventricle in this region. In electric Rays a pair of *electric lobes* (p. 192) are present at this point, and these enclose a mass of giant nerve-cells.

Ganoids.—The pallium covering the median telocœle consists mainly or entirely of epithelial and connective tissue elements, much as in Cyclostomes; and the telencephalon, which may be produced dorso-laterally into lobes (Fig. 159), gives rise anteriorly to cerebral hemispheres containing lateral ventricles and continuous with the olfactory lobes.

The well-developed diencephalon has a marked ventral flexure, and from its roof arises a strong pineal peduncle, the distal end of which extends into a hollow in the cranial roof, but undergoes atrophy in Amia, becoming completely separated off from the brain.[1] Well-marked lobi inferiores are present, and the hypophysis and saccus vasculosus are voluminous: the latter consists largely of glandular tubules which open into the infundibulum, as in Elasmobranchs.

The optic lobes are well-marked in most Ganoids. The large cerebellum gives rise to a *valvula cerebelli* (cf. Fig. 161) extending forwards into the ventricle of the mid-brain.

Except that only the median wall of the pallium is epithelial, the brain of Amia on the whole most nearly approaches that of the Teleosts in structure.

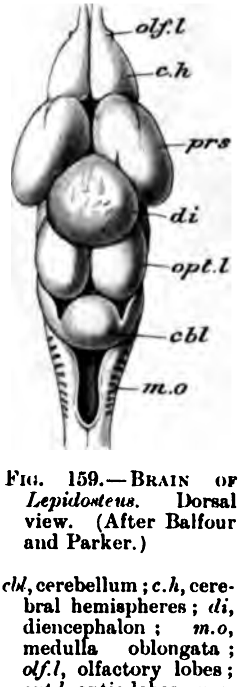

FIG. 159.—BRAIN OF *Lepidosteus*. Dorsal view. (After Balfour and Parker.)

cbl, cerebellum; *c.h*, cerebral hemispheres; *di*, diencephalon; *m.o*, medulla oblongata; *olf.l*, olfactory lobes; *opt.l*, optic lobes; *prs*, lobes of telencephalon.

Teleosts.—As is the case in many other Fishes, the brain in most Teleosts by no means fills the cranial cavity, and it is separated from the roof of the skull by a greater or less amount of a fat-like tissue and lymph: it never attains to so large a relative size as does that of Elasmobranchs. Its form varies greatly, more by far than in any other Vertebrate group, and only the following essential points can be mentioned here.

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[1] In Polypterus and Calamichthys the pineal body gives rise to a peculiar and extremely large epithelial vesicle, and the hypophysis communicates with the mouth-cavity by a hollow duct, even in the adult. The brain of these forms presents other special characters, and requires further investigation. In Devonian Ganoids, as well as in the Placoderms, there was a parietal foramen (p. 103).

The pallium is entirely epithelial in structure (Figs. 160—162): it presents no median involution dividing the anterior part of the telencephalon into two lateral hemispheres, and is therefore further reduced than in Ganoids: there is a median ventricle. The lower

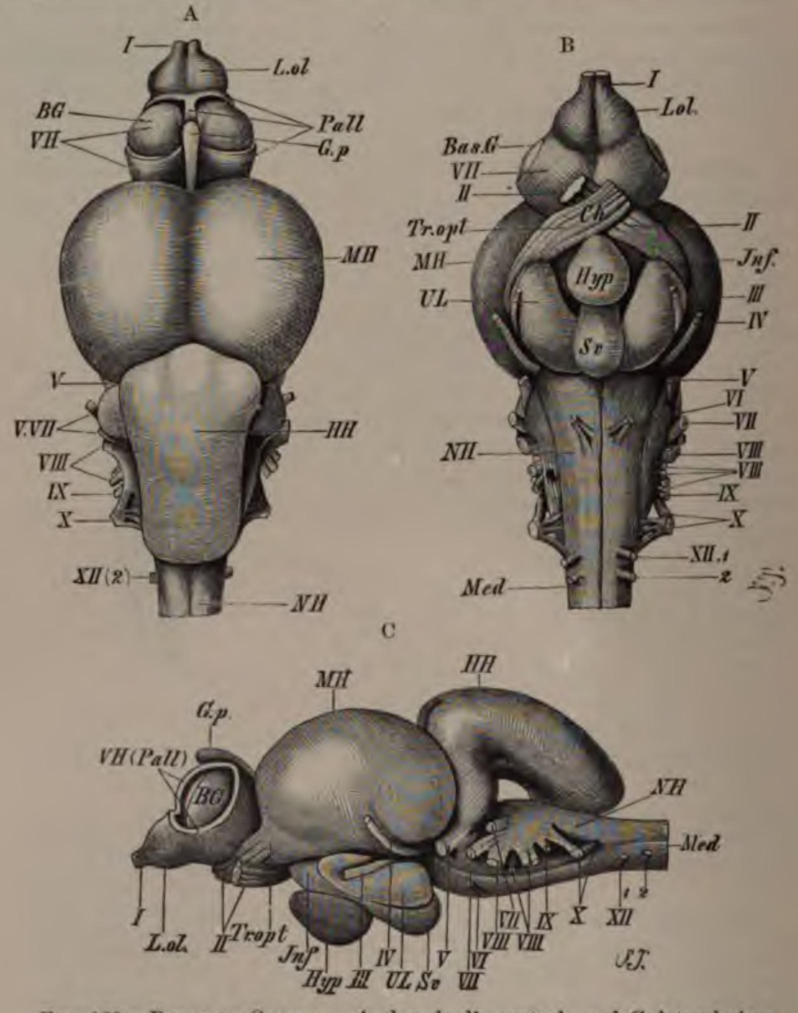

FIG. 160.—BRAIN OF SALMON. A, dorsal; B, ventral; and C, lateral view.

Ch, chiasma; *G.p*, pineal body; *HH*, cerebellum; *Hyp*, hypophysis; *Jnf*, infundibulum; *L.ol*, olfactory lobe; *Med*, spinal cord; *MH*, mid-brain; *NH*, medulla oblongata; *Pall*, pallium (in part removed), and *BG* and *BasG*, basal ganglia (corpora striata) of the telencephalon; *Sv*, saccus vasculosus; *Tr.opt*, optic tract; *UL*, lobi inferiores; *VH*, telencephalon; *I–X*, cerebral nerves; 1 and 2, first and second spinal nerves (the first represents the hypoglossal, *XII*).

part of the telencephalon consists of large paired basal ganglia (corpora striata) connected together by an anterior commissure The olfactory lobes are either closely applied to the telencephalon and contain a small ventricle, or they become differentiated into olfactory tract and bulb, as in Elasmobranchs.

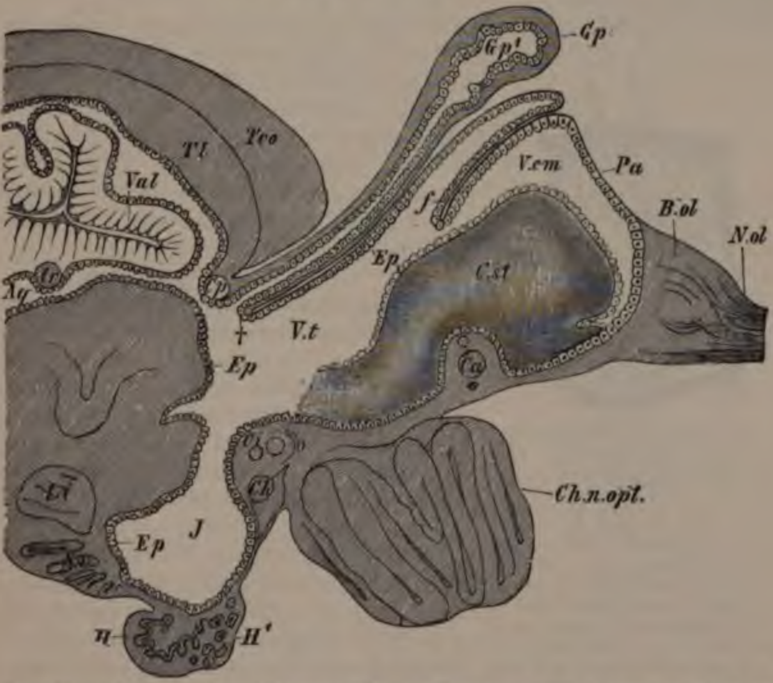

FIG. 161.—LONGITUDINAL VERTICAL SECTION THROUGH THE ANTERIOR PART OF THE TELEOSTEAN BRAIN. (Founded on a figure of the Trout's brain by Rabl-Rückhard.)

Aq, iter (mesocœle); *B.ol*, *N.ol*, olfactory lobe and nerve ; *Ca*, anterior commissure ; *Ch*, posterior optic ; *Ch.n.opt*, optic chiasma ; *Ci*, "inferior commissure" ; *Cp*, posterior commissure ; *C.st*, corpus striatum, which lies on either side of the middle line ; *Ep*, the epithelium (ependyme), lining the walls of the ventricles ; *Gp*, pineal body, with a cavity (Gp^1) in its interior ; *H*, H^1, hypophysis ; *J*, infundibulum ; *Li*, lobi inferiores ; *Sv*, saccus vasculosus ; *Tco*, roof of the optic lobes ; *Tl*, torus longitudinalis ; *tr*, pathetic nerve ; *Val*, valvula cerebelli ; *V.cm*, common ventricle of the secondary fore-brain (telocœle) ; *V.t*, third ventricle ; †, point at which the epithelial roof of the secondary fore-brain (pallium, *Pa*) becomes continuous with the lining of the anterior wall of the pineal tube ; above *f* is seen an outgrowth which represents a rudimentary parietal organ.

The diencephalon is very small, and is depressed between the telencephalon and mid-brain. The epiphysis (Figs. 160, 161) is plainly distinguishable, but it usually does not pass into the roof of the skull ; an outgrowth arising from the roof of the brain in front of the epiphysis represents the parietal organ, but this becomes constricted off from the brain and disappears during development.[1] Lobi inferiores, as well as a hypophysis and a glandular saccus vasculosus are present, but these vary much in the degree of their development. The saccus vasculosus here too, opens by several apertures into the infundibulum and is surrounded by a blood-sinus.

The mid-brain and cerebellum are extremely large relatively; the latter is bent upon itself, overlies the medulla oblongata behind, and is prolonged in front into the ventricle of the mid-brain as a *valvula cerebelli* (Fig. 161), as in Ganoids.

The Teleostean brain is a further specialisation of the type seen in Ganoids, and has no direct connection with that of Cyclostomes or Elasmobranchs.

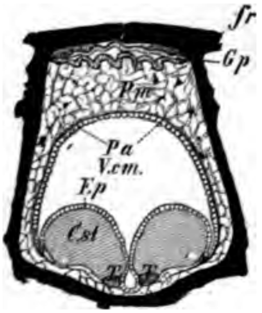

FIG. 162. — TRANSVERSE SECTION THROUGH THE FORE-PART OF THE TELEOSTEAN BRAIN.

C.st, corpora striata; *Ep*, ependyme; *fr*, frontal bone, underneath which the pineal tube, *Gp*, is visible in transverse section, and below this the perimeningeal tissue, *Pm*; *Pa*, the pallium, formed of a simple epithelial layer; *T*, *T*, olfactory tracts; *V.cm*, telocœle.

Dipnoans.—Both as regards external and internal structure, certain points of resemblance may be seen between the brain of Dipnoans and that of Elasmobranchs and Ganoids, but in other respects it is specialised. In Ceratodus, there is a considerable space between the walls of the cranium and the brain except in the region of the large olfactory lobes. The telencephalon is well developed, and the thin pallium, which is mainly nervous, is involuted along the median longitudinal line so as to completely separate the two hemispheres from one another dorsally in Protopterus and Lepidosiren: in Ceratodus they are partly united together dorsally and posteriorly by a narrow bridge formed by the choroid plexus. Olfactory lobes arise from the telencephalon anteriorly, and contain ventricles: in Ceratodus they overlie the hemispheres. Postero-laterally each hemisphere gives rise to a distinct *hippocampal lobe*. The pineal body has a long stalk, and its distal vesicle perforates the cartilaginous roof of the skull: in the embryo Ceratodus it even reaches as far as the integument. The complicated choroid plexus in this region gives rise to a large vesicle over which the pineal stalk extends. Lobi inferiores are present.

The well-marked mid-brain is indistinctly paired in Ceratodus, but is unpaired in Protopterus and Lepidosiren. The cerebellum is relatively much smaller than in Elasmobranchs and Teleosts: it gives rise to a valvula cerebelli, and a complicated choroid plexus roofs over the fourth ventricle.

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[1] A parietal foramen is present in the embryo in several Teleosts (*e.g.* Cottus, Salmo), and in some others (*e.g.* Callichthys) persists in the adult without a corresponding development of the pineal organ. In certain deep-sea forms (*e.g.* Argyropelecus, Cyclothone), however, the latter is comparatively complicated, and, as in Petromyzon, consists of two vesicles, showing regressive characters.

Amphibians.—The cerebral hemispheres of the Amphibia are distinguished from those of the Dipnoi by a higher development of the pallium, which, however, is differentiated even in the latter group into an external layer of nerve fibres and an internal cellular layer (central gray matter). The basal ganglia (corpora striata) are less marked, except in the Gymnophiona, and merely form a more or less prominent thickening of the wall of each hemisphere projecting into the lateral ventricle. A hippocampal lobe is not distinctly developed, but a *hippocampus* is represented by elevations of the central gray matter, which are connected right and left by a small *anterior pallial commissure* just above the anterior commissure (Fig. 164, D)

The Amphibian brain does not, however, lead directly towards that of Reptiles. Although the telencephalon is more highly differentiated than in lower forms, the diencephalon and mesencephalon are simpler than in Fishes; and, on the whole, the brain of Amphibians is less complicated than that of any other Vertebrates, except Lampreys.

In Urodeles the individual parts are more elongated and separated from one another than in Anurans, and the diencephalon is therefore more freely exposed. The hemispheres are almost cylindrical, and the olfactory lobes are distinct from one another, while in the Anura they are fused for a short distance anteriorly (Fig. 164). The diencephalon and optic lobes are much broader in Anurans than in Urodeles. The cerebellum consists simply of a small transverse fold, and is especially rudimentary in Urodeles.

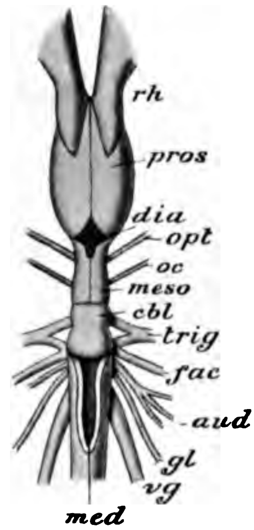

FIG. 163.—BRAIN OF *Ceratodus fosteri*. Dorsal view. (From Parker and Haswell's *Zoology*.)

aud, auditory nerve; *cbl*, cerebellum; *fac*, facial nerve; *gl*, glossopharyngeal; *med*, medulla oblongata; *mes*, mesencephalon; *oc*, oculomotor nerve; *opt*, optic nerve; *pros*, cerebral hemispheres; *rh*, olfactory lobes; *vg*, vagus nerve.

The infundibulum and hypophysis are well developed: a saccus vasculosus (infundibular gland) is no longer distinct as in Fishes, but is represented by the so-called infundibular process. The epiphysis does not extend beyond the skull in Urodeles, but in Anuran larvæ it reaches the integument, undergoing reduction later, when the bony skull-roof is formed; indications of its extracranial portion can, however, be more or less distinctly

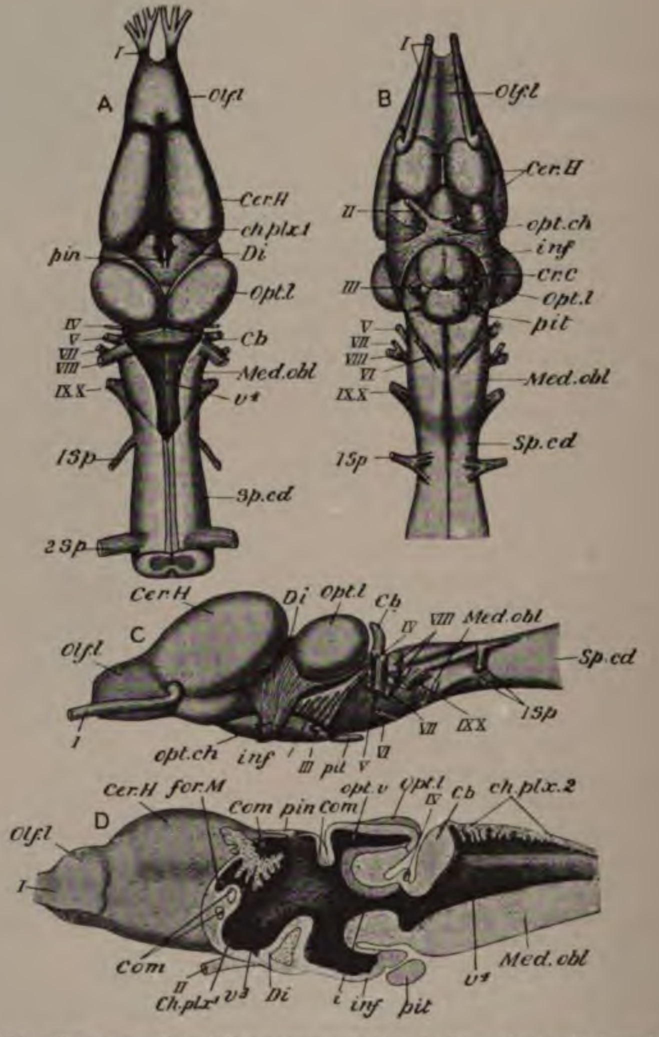

FIG. 164.—BRAIN OF FROG [(*Rana temporaria*). A, from above; B, from below; C, from the side; D, in longitudinal vertical section. (A—C, after Gaupp; D, after Osborn.)

Cb, cerebellum; *Cer.H*, cerebral hemispheres; *ch.plx*^{1}, in A, paraphysis, in D, anteroid choroid plexus (removed in A); *ch.plx*^{2}, posterior choroid plexus (tela choroidea); *Com* (above), superior and posterior commissures; *Com* (below), anterior commissure and anterior pallial commissure just above it; *Cr.C*, crura cerebri; *Di*, diencephalon; *for.M*, foramen of Monro; *i*, iter; *inf*, infundibulum; *Med.obl*, medulla oblongata; *Olf.l*, olfactory lobe; *opt.ch*, optic chiasma; *Opt.l*, optic lobe; *opt.v*, optic ventricle; *pin*, stalk pineal of body; *pit*, pituitary body; *Sp.cd*, spinal cord; v^3, third ventricle; v^4, fourth ventricle; I–X, cerebral nerves; 1 *Sp*, 2 *Sp*, first and second (=embryonic second and third) spinal nerves.

recognised even in the adult as a "brow-spot": thus its intracranial portion does not represent the entire epiphysis.[1] A parietal organ appears to be entirely wanting in all Amphibians with the possible exception of some few Anura, in which traces of it have been described.[2]

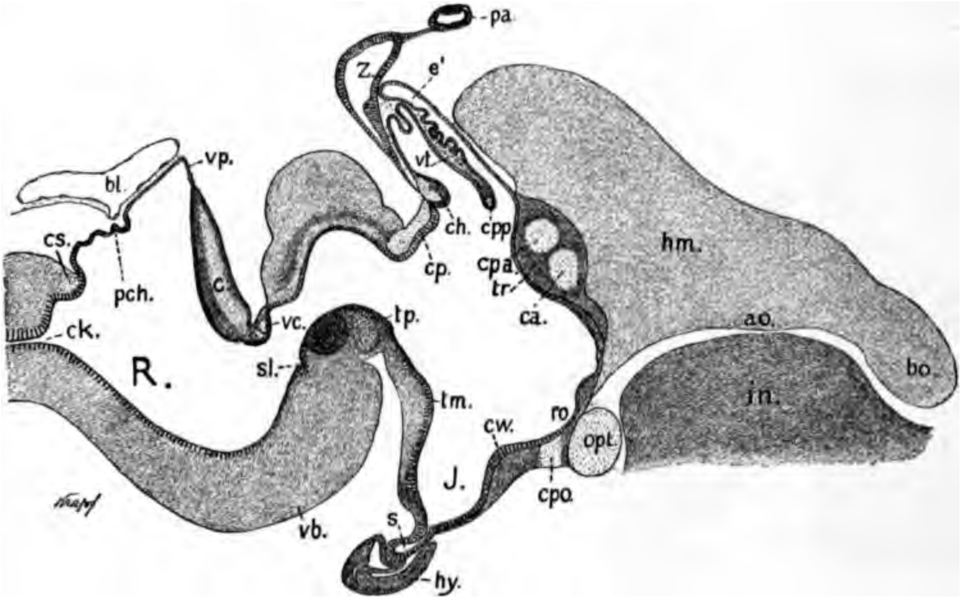

Fig. 165.—Longitudinal Section of Brain of an Embryo of *Lacerta vivipara* × 26. (After K. von Kupffer.)

ao, olfactory area ; *bl*, blood-sinus ; *bo*, olfactory lobe ; *c*, cerebellar commissures ; *ca*, anterior commissure ; *ch*, superior (habenular) commissure ; *ck*, central canal of spinal cord ; *cp*, posterior commissure ; *cpa*, anterior pallial (hippocampal) commissure ; *cpo*, posterior optic commissure ; *cpp*, posterior pallial commissure ; *cs*, spinal commissure ; *cw*, swelling of optic chiasma ; e^1, paraphysis ; *hm*, cerebral hemisphere ; *hy*, hypophysis ; *in*, interorbital septum ; *J* (and *s*) ventricle of infundibulum ; *opt*, optic chiasma ; *pa*, parietal organ ; *pch*, choroid plexus on medulla oblongata ; *R*, hind-brain ; *ro*, optic recess ; *sl*, sulcus intraencephalicus posterior ; *tp*, tuberculum posterius superius : *tr*, torus transversus ; *vb*, ventral flexure of medulla oblongata ; *vc*, valvula cerebelli ; *vp*, posterior medullary velum ; *vt*, velum transversum ; *Z*, epiphysis.

In the Gymnophiona the olfactory lobes and hemispheres are relatively larger than in other Amphibians, and the hemispheres overlap the posterior parts of the brain to a larger extent. The

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[1] A rounded vascular body arising from the roof of the third ventricle and representing a paraphysis (p. 200) has been mistaken for the epiphysis (Fig. 164, A, *ch. plx′*).

[2] A parietal foramen was, however, present in the Palæozoic *Stegocephali* and other extinct Amphibia.

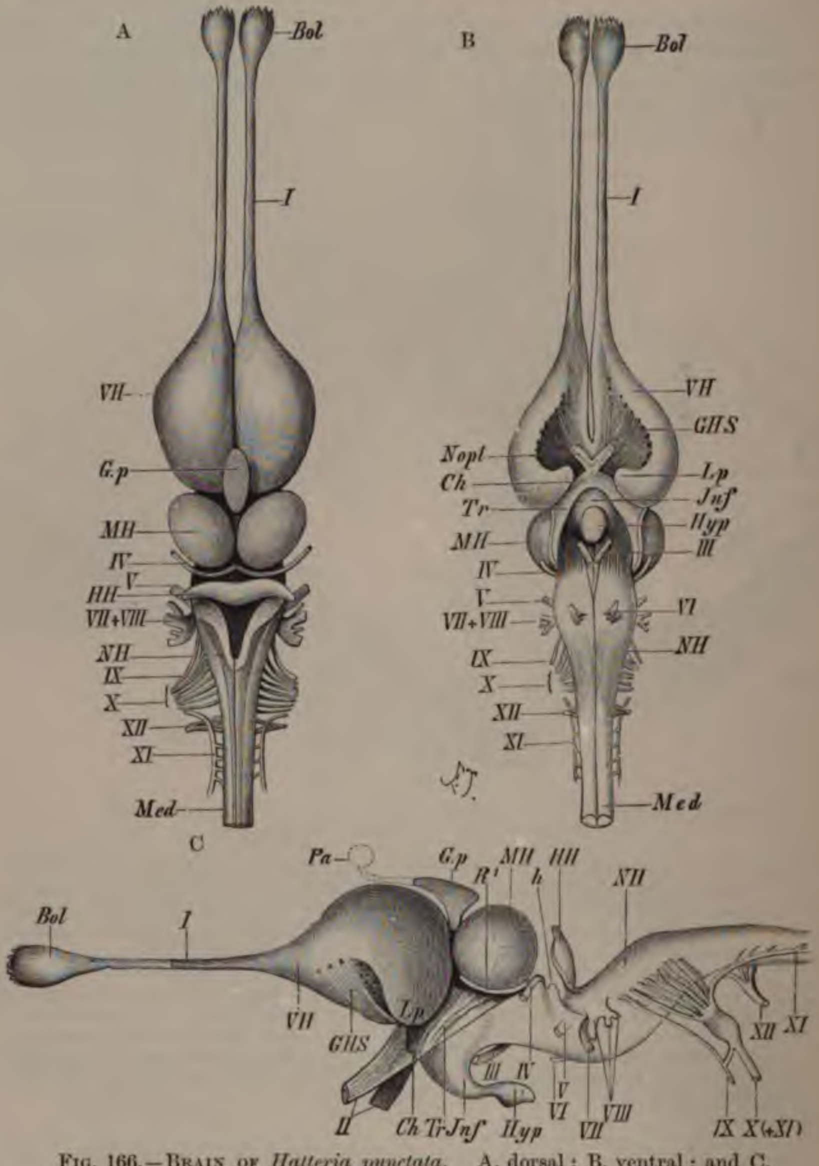

FIG. 166.—BRAIN OF *Hatteria punctata*. A, dorsal; B, ventral; and C, lateral view.

Bol, olfactory bulb; *Ch*, optic chiasma; *GHS*, cerebral peduncles; *G.p*, pineal body, shown in C continuous with the parietal eye (*Pa*), and only indicated diagrammatically in A; *h*, small elevation in front of the cerebellum; *HH*, cerebellum; *Hyp*, hypophysis; *Inf*, infundibulum; *Lp*, process of the hemisphere representing a hippocampal lobe; between *Lp* and *GHS* is a deep groove (*fovea limbica*) between the olfactory lobe and pallium; *Med*, spinal cord; *MH*, optic lobes; *NH*, medulla oblongata; *Nopt*, optic nerve; R^1, curved ridge at the base of the optic lobe; *Tr*, optic tract; *VH*, cerebral hemispheres; *I-XII*, cerebral nerves.

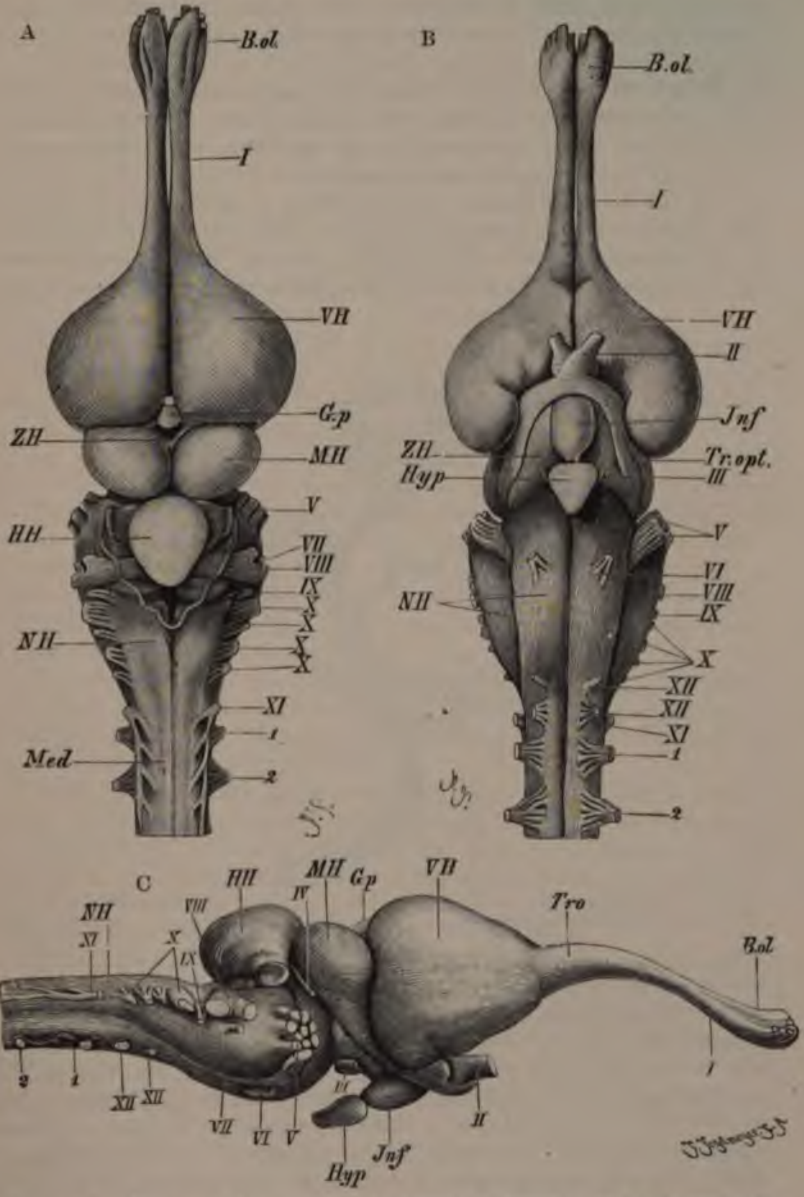

FIG. 167.—BRAIN OF ALLIGATOR. A, dorsal; B, ventral; and C, lateral view.

B.ol, olfactory bulb; *G.p*, pineal body; *HH*, cerebellum; *Hyp*, hypophysis; *Jnf*, infundibulum; *Med*, spinal cord; *MH*, optic lobes; *NH*, medulla oblongata; *Tro*, olfactory tract; *VH*, cerebral hemispheres, each of which gives rise postero-laterally to a hippocampal lobe partially overlying the corresponding optic tract, *Tr.opt*; *ZH*, diencephalon; *I-XII*, cerebral nerves; 1, 2, first and second spinal nerves.

infundibulum and hypophysis extend far backwards: details regarding the pineal apparatus are not known.

Reptiles.—The brain of Reptiles reaches a considerably higher stage of development than that of the forms already described, and the individual parts overlie one another to a greater extent, especially in the Agamæ and Ascalabotæ.

In the brain of Dipnoi and Amphibia there are comparatively few cellular elements in the outer layer of the pallium, and the larger masses of cells (central gray matter) line the ventricles: in the Reptilia a peripheral shifting takes place, giving rise to the formation of a definite *cortex*, containing the characteristic pyramidal cells such as are present in all the higher Vertebrates. It appears that the first differentiation of a cortex phylogenetically was connected with the olfactory sense: while in Fishes, for example, the olfactory tracts terminate in the corpora striata, most of their fibres extend into a definite region of the pallium from Reptiles onwards. Thus an " olfactory cortex " is formed, to which other centres are gradually added in the ascending series of Vertebrates.

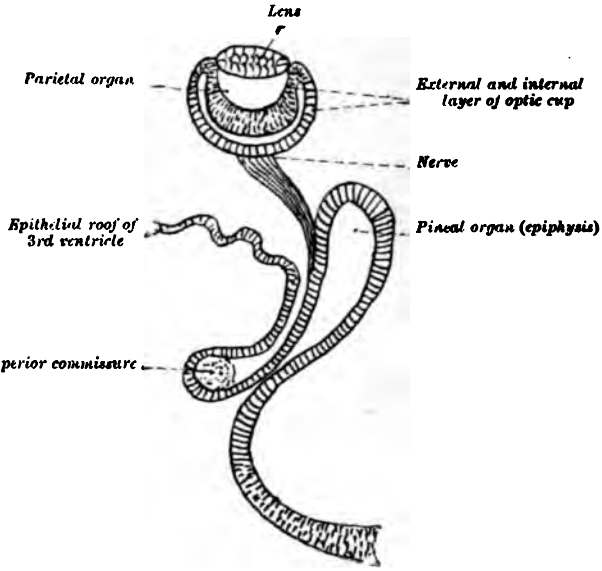
Lens
Parietal organ
External and internal layer of optic cup
Nerve
Epithelial roof of 3rd ventricle
Pineal organ (epiphysis)
Superior commissure

Fig. 168.—Sketch of the Pineal Apparatus of Hatteria. (After Dendy.)

The pallial commissures (Fig. 165), like those of Amphibians, are not large relatively, but in addition to an anterior pallial or hippocampal commissure, traces are present of a so-called "*fornix*" (posterior pallial commissure, p. 201); the hippocampal lobes with their choroid plexuses are much more distinct in many cases (*e.g.* Hatteria, Chelonia, Crocodilia).

The olfactory lobes may be closely applied to the hemispheres (*e.g.* Anguis, Amphisbæna, Typhlops), or may consist of a well-marked olfactory tract, passing anteriorly into an olfactory bulb from which the nerves of smell arise (*e.g.* Hatteria, Lacerta, Crocodilus). Olfactory ventricles are usually present.

The diencephalon is always depressed, and is hardly, or not at all, visible from the dorsal side. A distinct hypophysis and infundibulum as well as an epiphysis are present, and in most Lizards the parietal organ (cf. p. 202) retains more or less distinctly, even in the adult, the structure of a median eye.[1]

This *parietal eye* (Fig. 168) is situated in the parietal foramen of the skull, and is in close connection with the more posteriorly situated pineal organ, though in the embryo the nerve which supplies it is seen to arise independently from the brain, in front of the pineal outgrowth. It has the form of a vesicle, the dorsal wall of which may become thickened to form a transparent lens-like body, while the rest of the wall consists of several layers and forms a pigmented "retina," with which the more or less rudimentary nerve is continuous. The vesicle is surrounded by a vascular connective tissue capsule, and in many cases the integument immediately overlying it is pigmentless and transparent, forming a kind of cornea. Traces of a vitreous body have also been observed.[2] Various degrees of reduction of the "retina" and other parts as they occur, *e.g.* in Hatteria, are seen amongst Lizards (*e.g.* Lacerta, Anguis), and the organ may be recognised in a simpler form in embryo Snakes.

As in all the Amniota, two chief divisions can usually be recognised in the infundibulum of Reptiles: a dorsal vascular and glandular body, corresponding to the saccus vasculosus of the Anamnia, and a more ventral infundibular portion, the glandular character of which is still retained to some extent in the Sauropsida, but there is no opening into the ventricular cavity.

In the mid-brain the two well-marked optic lobes in some cases show indications of a further subdivision into four; from them the optic tracts pass downwards and forwards to the chiasma. The cerebellum is relatively small, except in the Crocodilia (Fig. 167), in which it consists of a thicker median lobe, and of two lateral portions. The medulla oblongata has a marked ventral flexure.

Birds.—The avian brain (Fig. 169) is of a very peculiar type: it has few points of resemblance to that of Mammals, and is very different from that of Reptiles, though especially as regards its individual sections it is more or less comparable to that of certain of the latter (*e.g.* Chelonia). The basal ganglia (corpora striata) of

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[1] A parietal organ is wanting in Gecko, Ameida and Tejus, and there is no pineal organ in the Crocodile.

[2] The paraphysis gradually extends beneath the epiphysial outgrowth, and forms a sort of cushion under the parietal eye.

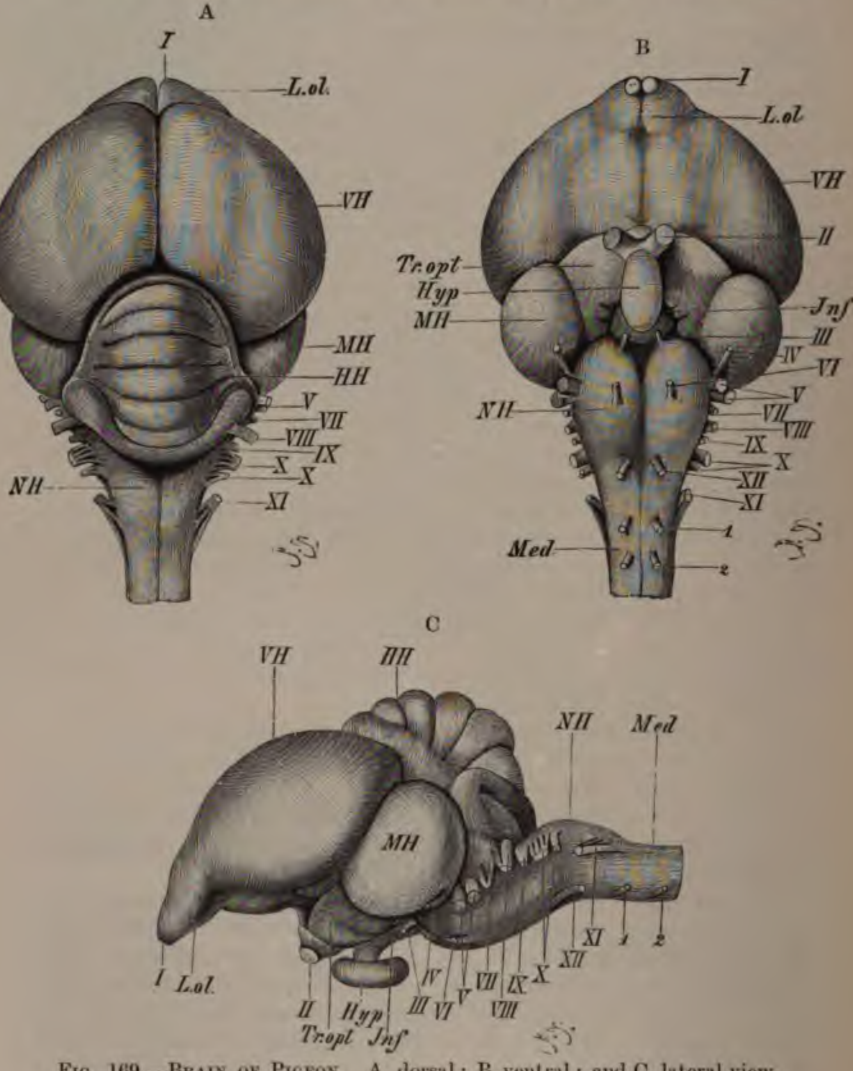

FIG. 169.—BRAIN OF PIGEON. A, dorsal; B, ventral; and C, lateral view.

HH, cerebellum; *Hyp*, hypophysis; *Inf*, infundibulum; *L.ol*, olfactory lobes; *Med*, spinal cord; *MH*, optic lobes; *NH*, medulla oblongata; *Tr.opt*, optic tract; *VH*, cerebral hemispheres; *I-XII*, cerebral nerves; 1, 2, first and second spinal nerves.

the hemispheres reach a relatively larger size in Birds than in any other Vertebrates. An advance on Reptiles is seen in the connections of the pallial cortex in various directions, and in many Birds indications of cortical centres can already be recognised.

In the well-developed hemispheres frontal, parietal, and temporal regions can be recognised: their surface is perfectly smooth, and the lateral ventricles are not extensive. The different parts of the brain overlie one another much more markedly than in any Reptile, and the hemispheres are much larger relatively, covering over the diencephalon and part of the mid-brain. The olfactory lobes are

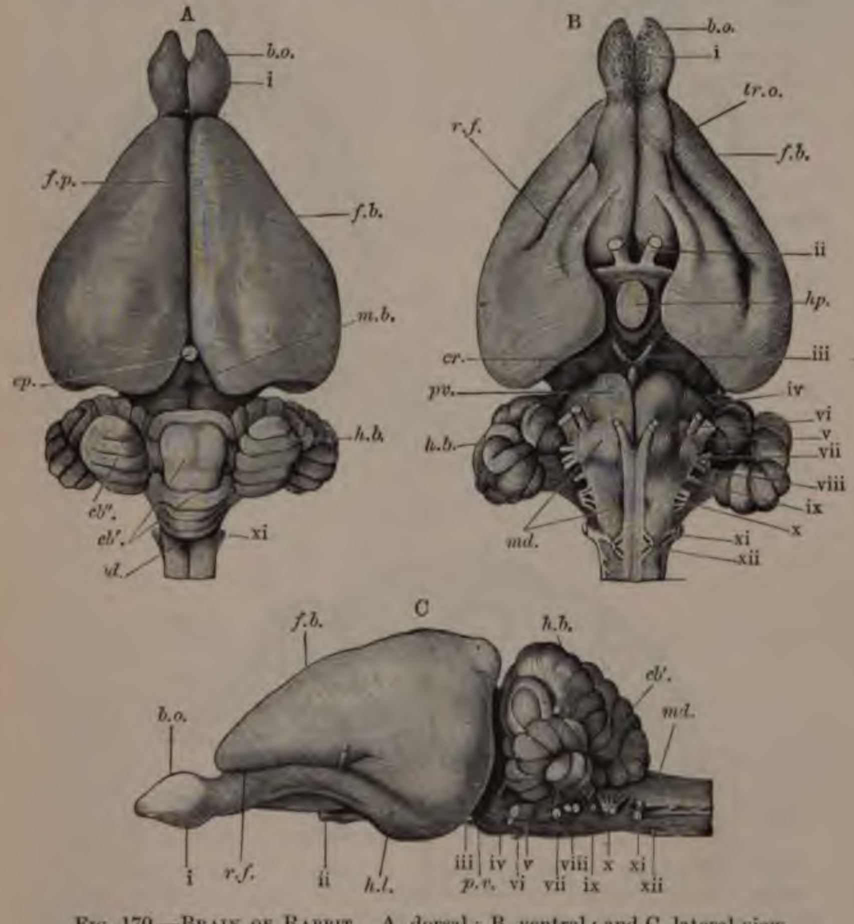

Fig. 170.—Brain of Rabbit. A, dorsal ; B, ventral ; and C, lateral view.

b.o, olfactory bulb ; *cb′* superior vermis, and *cb″*, lateral lobe of cerebellum ; *cr*, crura cerebri ; *ep*, pineal body ; *f.b*, cerebral hemispheres ; *f.p*, pallial fissure ; *h.b*, cerebellum ; *h.l*, hippocampal lobe ; *hp*, hypophysis ; *m.b*, optic lobes ; *m.d*, medulla oblongata ; *p.v*, pons Varolii ; *r.f*, rhinal fissure ; *tr.o*, olfactory tract ; i-xii, cerebral nerves.

poorly developed.[1] The distal enlarged end of the pineal body extends as far as the dura mater, and the structure of the internal

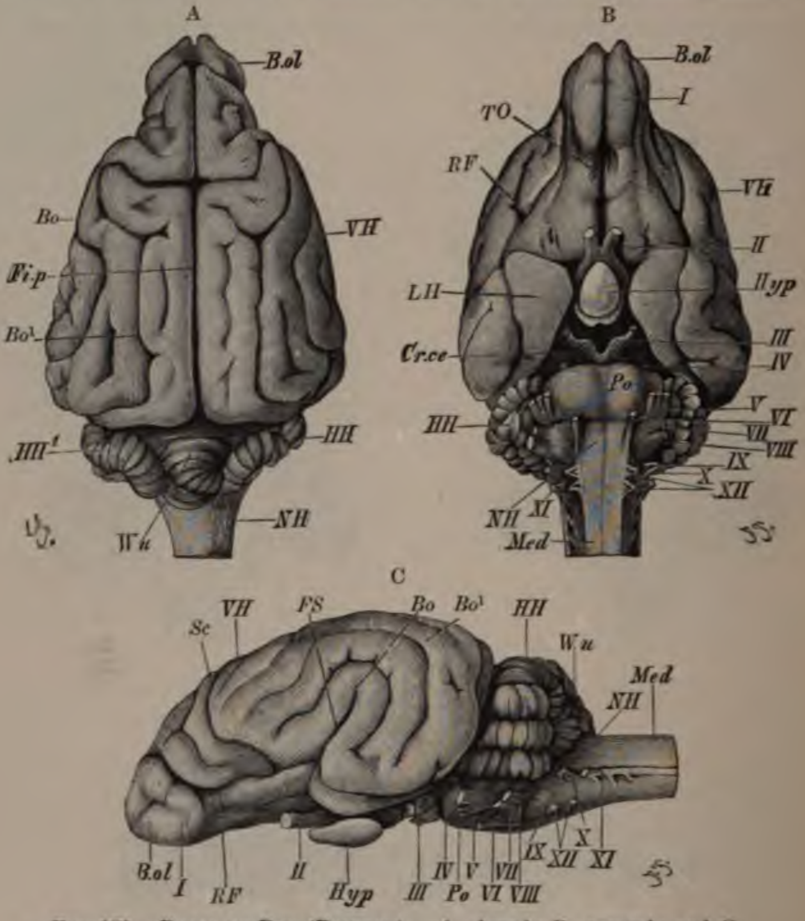

FIG. 171.—BRAIN OF DOG (POINTER). A, dorsal; B, ventral; and C, lateral view.

Bo, *Bo*^{1}, arcuate fissures ; *B.ol*, olfactory bulb ; *Cr.ce*, crura cerebri ; *Fi.p*, pallial fissure ; *FS*, Sylvian fissure ; *HH*, lateral lobe, and *HH*^{1}, flocculus of cerebellum ; *Hyp*, hypophysis ; *LH*, hippocampal lobe ; *Med*, spinal cord ; *NH*, medulla oblongata ; *Po*, pons Varolii ; *RF*, rhinal fissure ; *Sc*, sulcus cruciatus ; *TO*, olfactory tract ; *VH*, cerebral hemispheres ; *Wu*, superior vermis ; *I-XII*, cerebral nerves.

part of the organ resembles that of a tubular gland, penetrated by fibrous tissue and blood-vessels. There is no trace of a parietal organ.

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[1] The toothed Birds of the Cretaceous period, with Hesperornis at their head, possessed a very lowly organised, reptilian form of brain, with small *hemispheres and large* olfactory lobes.

The cerebellum consists of a well-developed and folded median lobe, and of two lateral portions (flocculi), which vary much both in form and size. Posteriorly it completely covers the fourth ventricle. The two optic lobes, in which, as in certain Reptiles, a subdivision is indicated, are separated from one another and pressed downwards, so as to lie at the sides of the brain in the angle between the hemispheres, cerebellum, and medulla oblongata, and they are connected by a broad commissure. The ventral side of the short medulla shows a marked flexure, bending upwards to the spinal cord.

Mammals.—The brain in embryo Mammalia is very similar to that of the Sauropsida, but the subsequent differentiation of its parts, and more particularly that of the pallium, gives it a very special character. The cerebral cortex becomes much more highly developed and in many Mammals is more or less markedly convoluted[1] (Figs. 171 and 173, B). In others, again, the surface of the hemispheres remains smooth (Fig. 170), but a subdivision into lobes (frontal, parietal, occipital, and temporal), as well as certain fissures (*e.g.* rhinal, hippocampal, callosal) can always be recognised to a greater or less extent, and the hemispheres are relatively so large as to cover over the more posterior parts of the brain ; in some of the lower forms, the mid-brain can still be seen from above, while in the higher types

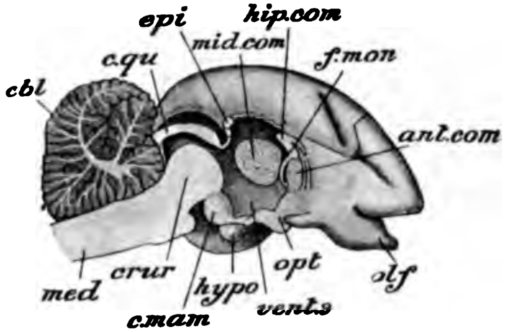

Fig. 172.—Longitudinal Section of Brain of Rock Wallaby (*Petrogale penicillata*). (From Parker and Haswell's *Zoology*.)

ant.com, anterior commissure ; *cbl*, cerebellum ; *c.mam*, corpus mammillare ; *c.qu*, optic lobes ; *crur*, crura cerebri ; *epi*, epiphysis, with the posterior commissure immediately behind it ; *f.mon*, position of foramen of Monro ; *hip.com*, hippocampal commissure, consisting here of two layers, continuous at a posterior bend, the splenium, somewhat divergent in front where the septum lucidum extends between them ; *hypo*, hypophysis ; *med*, medulla oblongata ; *mid.com*, middle commissure ; *olf*, olfactory lobe ; *opt*, optic chiasma ; *vent.*3, third ventricle.

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[1] It is only possible to homologise the *main* sulci to a greater or less extent amongst the various types of convolution seen in the Mammalian brain (cf. p. 228).

(Primates) even part of the cerebellum is hidden (Figs. 173, A and B), although this is to a greater extent the case in some of the lower Apes, with smooth hemispheres (*e.g.* Hapale, Chrysothrix), than in Man. No satisfactory explanation has so far been given for the different degrees of convolution seen amongst Mammals: as a general rule, the brain in lower and smaller types (except, *e.g.* in Echidna) is less convoluted than in higher and larger ones.

The number of fibres radiating from the cortex (*corona radiata*) is very small in lower types (*e.g.* Rodents), and largest in Man. A complex network of fibres in the cortex itself connects its various parts together, and other strong bundles extend through the hemispheres connecting individual regions of the pallium with one another. The commissures between the hemispheres known as the *corpus callosum* and *fornix* (Fig. 173, A) are also much more highly developed than in other Vertebrates. The former is an important structure in the higher Mammalia, its development corresponding to that of the pallium: it extends upwards and then backwards from the region of the lamina terminalis in the form of a thin plate, and reaches its highest development in Primates. A corpus callosum is apparently wanting in Monotremes and Marsupials, in which a *hippocampal commissure* is present in the position of the body of the fornix, just above the anterior

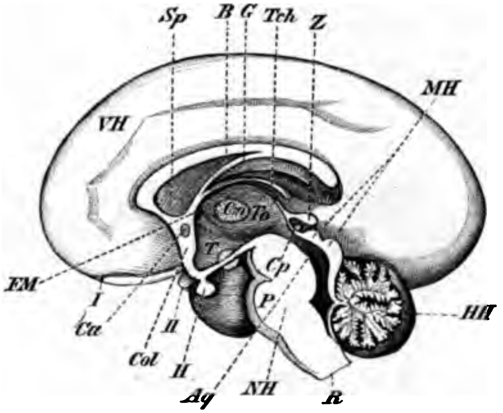

FIG. 173A.—HUMAN BRAIN. Median longitudinal vertical section. (Mainly after Reichert.)

corpus callosum ; *G*, fornix, which extends antero-ventrally to the lamina terminalis (*Col*), in the upper part of which is seen the anterior commissure (*Ca*), and between the latter and the optic thalami (*To*) the foramen of Monro (*FM*) ; *H*, pituitary body ; *HH*, cerebellum ; *MH*, corpora bigemina, with the iter (*Aq*), anterior to which is seen the posterior commissure (*Cp*) ; *NH*, medulla oblongata, with the pons Varolii (*P*) ; *R*, spinal cord ; *T*, infundibulum ; *Tch*, tela choroidea ; *To*, optic thalamus (diencephalon), with the middle commissure (*Cm*) ; *VH*, cerebral hemisphere ; *Z*, pineal body ; *I*, olfactory nerve ; *II*, optic nerve.

commissure (Fig. 172, and cf. pp. 201 and 220), and the brain of these forms remains at a comparatively low stage of development: the anterior (basal) commissure is comparatively large, whereas in the Eutheria its relative size is in inverse proportion to that of the more important corpus callosum. In Edentates the brain is also of a low type, and the same is true of that of Rodents, Insectivores, and Bats, though a considerable advance is here seen as compared with Marsupials. A large *middle commissure* connects the two optic thalami.

In addition to the lobes mentioned above, a *central lobe* of the hemispheres is present in Primates, and increases in development in passing from the Gibbon, Orang, Chimpanzee, and Gorilla, up to Man. But there is no justification for the statement that "the human brain is only an enlarged anthropoid brain," for in the former a number of entirely new regions have been acquired, especially as regards the frontal, temporal, and central lobes, which have consequently undergone extension.

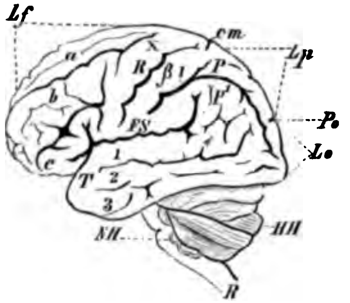

Fig. 173b.—Convolutions of the Human Brain. (After A. Ecker.)

a, *b*, *c*, superior, middle, and inferior frontal gyri; *cm*, the calloso-marginal sulcus on the dorsal surface; *FS*, Sylvian fissure; *HH*, cerebellum; *Lf*, frontal lobe; *Lo*, occipital lobe; *Lp*, parietal lobe; *NH*, medulla oblongata; *Po*, parieto-occipital fissure; *P*, *P*¹, superior and inferior parietal gyri separated from one another by the interparietal fissure (*I*); *R*, spinal cord; *T*, temporal lobe; *X*, β I, anterior and posterior central convolutions, separated from one another by the fissure of Rolando (*R*); 1 to 3, superior, middle, and inferior temporal convolutions.

In correspondence with the division of the hemispheres into lobes, there is a differentiation of the lateral ventricles,[1] so that an *anterior*, a *posterior*, and an *inferior cornu* can be distinguished in each; the inferior cornu extends into the temporal portion, which corresponds to the hippocampal lobe of Reptiles, and an eminence on its floor, the *hippocampus major*,[2] formed as an involution of the median wall of the hemisphere, is much more marked than in lower forms: the line of involution is known as the hippocampal fissure.

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[1] The ventricles are lined by epithelium (ependyme), which, strengthened by connective tissue layers derived from the pia mater (*telæ choroideæ*), also forms the roofs of the third and fourth ventricles and extends into the lateral ventricles as *plexus choroidei*.

[2] The hippocampal system has important relations to the olfactory centre. The *gyrus dentatus* (*fascia dentata*) and the *fimbria* arise in close connection with the hippocampus, the fimbria having intimate relations to the fornix.

The central olfactory apparatus (*rhinencephalon*) in its entirety is represented by the olfactory bulb, peduncle, and tubercle, the piriform lobe, and the hippocampus, and is separated from the pallium by the *rhinal fissure* (Figs. 170, 171). This fissure is in close relation to the *splenial* (*callosal*) fissure, which bounds the *supracallosal* gyrus dorsally, extending more or less parallel to the corpus callosum. The *Sylvian* fossa or fissure is also a typical fissure: it is situated at about the middle of the rhinal fissure, and in the higher Mammals is overlapped by the pallium so that the fossa is converted into a fissure. In Carnivores, Cetaceans, and Ungulates, three gyri arch over the Sylvian fissure, one above the other, and are separated by the so-called *arcuate* fissures (Fig. 171). The upper of these, bounded above by the *longitudinal pallial* fissure, is spoken of as the *marginal* gyrus. Along the lateral surface of the hemisphere, the *cruciate* sulcus (the homologue of the central sulcus or *fissure of Rolando* of Primates) extends upwards to the pallial fissure. Characteristic of the brains of all Apes excepting those with smooth hemispheres is the *parieto-occipital* sulcus, between the parietal and occipital lobes: in Man, the lateral parts of this fissure are more or less indistinct (cf. 173, B, in which other gyri and sulci of the human brain are shown).

The corpus striatum is surrounded and perforated by fibres passing down from the pallium (anterior limb of the *internal capsule* of Primates). Unlike the corresponding structure in other Vertebrates, the corpus striatum of Mammals becomes gradually more deeply situated, and is comparatively small as compared with the rest of the brain.

The olfactory lobes usually extend forwards freely from the base of the telencephalon, and each may retain throughout life a prolongation of the lateral ventricle (*e.g.* Perissodactyles); in some cases (*e.g.* numerous aquatic forms and Primates) they are completely covered by the frontal lobes. The degree of their development is in proportion to that of the olfactory sense, and they may even be entirely reduced (cf. under Olfactory Organ).

The pineal body is displaced downwards by the hemispheres and lies against the anterior lobes of the mid-brain, not reaching to the roof of the skull and brain-membranes. Its bifurcated peduncle connects it with the roof of the diencephalon and contains nervous substance: its distal end has the form of a rounded or oval sac, consisting of compact epithelial tissue and containing concretions. A parietal organ is wanting. Traces of the saccus vasculosus and lobi inferiores still occur, even in Man, in connection with the infundibulum.

The mid-brain (corpora bigemina) is of smaller relative size than in other Vertebrates. A transverse furrow across the solid optic lobes subdivides them into an anterior larger and a posterior smaller pair of lobes (cf. p. 221).

The division of the large cerebellum into a median and two lateral portions, already indicated in Reptiles, is carried to a still further extent in Mammals. The median portion gives rise to the so-called *superior vermis*, while the lateral parts form the *lateral lobes* and *flocculi* (Figs. 170, 171). In Carnivores, certain Edentates, Pigs, and Lemurs, the vermis is relatively large as compared with the lateral portions; while in Cetaceans, Elephants, Apes, and Man the latter are more highly developed and the median lobe reduced. The two lateral lobes of the cerebellum are connected by a large commissure, the *pons Varolii*: this extends round the medulla oblongata ventrally, and is more largely developed the higher we pass in the mammalian series. Other bands of nerve-fibres connecting the cerebellum with various parts of the brain are spoken of as the anterior, middle, and posterior peduncles of the cerebellum, the relations of which, and of the crura cerebri, are indicated in Fig. 174.

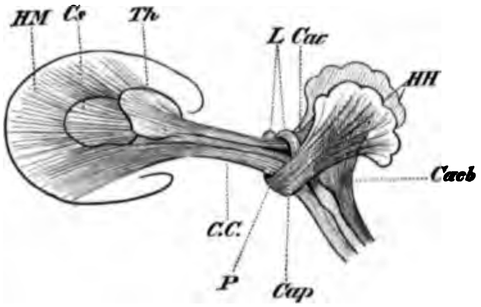

FIG. 174.—DIAGRAM OF THE CHIEF SYSTEMS OF FIBRES OF THE MAMMALIAN (HUMAN) BRAIN. (From a drawing by A. Ecker.)

Cac, crura cerebelli ad corpora bigemina; *Cacb*, crura medulla ad cerebellum; *Cap*, crura cerebelli ad pontem; *CC*, crura (pedunculi) cerebri; *CS*, corpus striatum; *HH*, cerebellum; *HM*, hemisphere; *L*, lemniscus: *P*, pons; *Th*, optic thalamus.

A study of the brain-casts in certain North American Eocene forms is very instructive from an evolutional point of view, and shows that the brain, and more especially the fore-brain, in these animals was of extremely small size relatively (Fig. 175). The brain of Dinoceras mirabile might easily be mistaken for that of a Lizard, and was so small that it could easily be drawn through the greater part of the neural canal: in the Cretaceous Dinosaurian Triceratops, the brain was apparently still smaller relatively. The olfactory nerves were extremely well developed in these forms.

In connection with the importance of the brain in modelling the form of the skull, it may be mentioned that in many Mammals, including Man, the outer surface of the skull in various parts shows a kind of relief of certain underlying portions of the brain. In some cases, only the larger divisions of the brain (cerebrum and cerebellum) are thus indicated externally: in others, a relief of the convolutions is also seen, and in Mustela and Lutra, for example, it is almost complete on the lateral portions of the skull

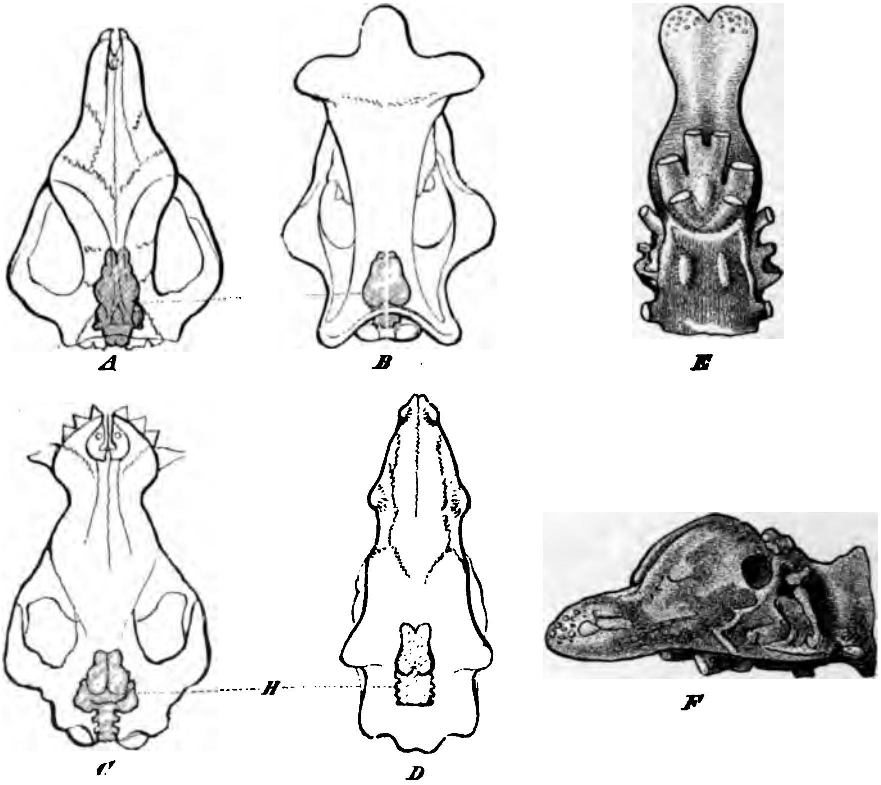

Fig. 175.—Casts of the Brains of Various Eocene Mammals. (After Marsh.)

Skull, with brain indicated, of *A*, *Tillotherium fodium*; *B*, *Brontotherium ingens*; *C*, *Coryphodon hamatus*; and *D*, *Dinoceras mirabile*. *E* and *F*, ventral and lateral views of the brain of *Dinoceras mirabile*.

covered by the temporal muscles, and may even extend dorsally to the middle line.

II. PERIPHERAL NERVOUS SYSTEM.

Two principal groups of peripheral nerves may be distinguished, viz., **spinal** and **cerebral**, that is, those which arise from the *spinal cord* and brain respectively: between them is an inter-

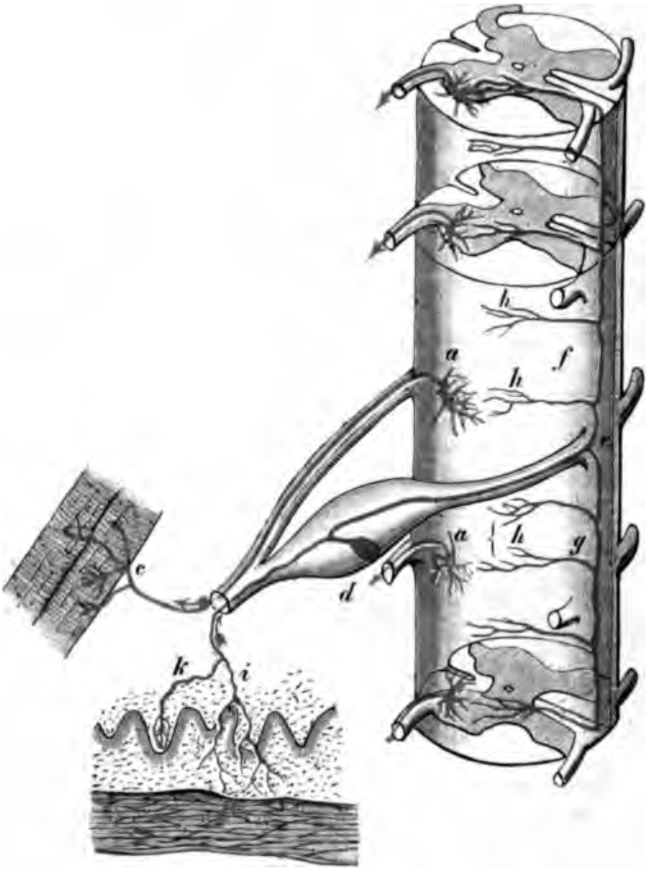

FIG. 176.—DIAGRAM ILLUSTRATING THE ORIGIN, COURSE, AND TERMINATION OF THE MOTOR AND SENSORY FIBRES OF THE SPINAL NERVES, AS WELL AS THE RELATIONS OF THE SENSORY COLLATERAL FIBRES TO THE POINTS OF ORIGIN OF THE VENTRAL ROOTS. (After M. v. Lenhossék.)

The spinal cord is shown as if transparent. The fibres of the ventral roots arise from the motor cells of the ventral cornua of the gray matter (*a*) and end in fine branches on the striated muscle-fibres (*c*). The spinal ganglion (*d*) is shown relatively much larger than in reality, and in it only a single unipolar nerve-cell is represented: the centripetal fibre of the latter is seen entering the dorsal root, and at *e* bifurcates in the spinal cord into an anterior (*f*) and a posterior (*g*) branch, each of which ends freely in the gray substance, first giving off numerous collateral fibres (*h*). The centrifugal fibre of the cell in the spinal ganglion forms a peripheral sensory fibre extending to the skin, where part of it is shown ending in fine branches in the epidermis (*i*), another part forming a coil in connection with a tactile corpuscle (*k*).

mediate group known as the *spino-occipital nerves.* By their means a physiological connection is established between the periphery of the body and the central nervous system both in centripetal and centrifugal directions.

The spinal nerves retain the more primitive and simple relations, and all show a similar arrangement along both dorsal and ventral regions of the spinal cord, so that each segment of the trunk possesses a *dorsal* and a *ventral* pair. The former consist mainly of *afferent* (centripetal) or *sensory*, the latter of *efferent* (centrifugal) or *motor* fibres (Fig. 176).

Each dorsal or sensory nerve has a *ganglion* in connection with it, while on the ventral nerves a ganglion is wanting, except in the embryo of certain Fishes. The ventral nerves, which mainly supply the great lateral muscles of the trunk and their derivatives, arise as direct outgrowths from the spinal cord, while the dorsal nerves first appear as outgrowths from their ganglia, coming into connection with the cord secondarily. The ganglia themselves are developed from a *neural ridge* of ectoderm cells lying close to the junction of the medullary cord and outer ectoderm (Fig. 177). On the distal side of each ganglion, both nerve-roots almost always become bound up in a common sheath, though many facts seem to indicate that in the ancestors of existing Vertebrates the dorsal and ventral roots remained distinct, as in fact is still the case in Amphioxus and Petromyzon.

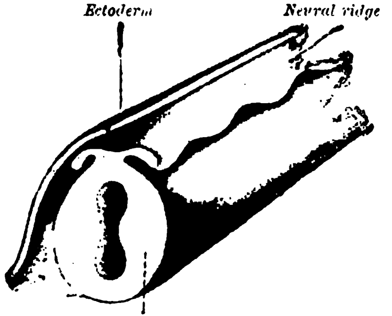

Fig. 177.—Diagram of the Embryonic Spinal Cord and the Neural Ridge from which the Spinal Ganglia are Differentiated. (After J. S. Kingsley.)

In addition to the *somatic* afferent and efferent fibres, which innervate the skin and muscles of the dorsal and lateral portions of the myotomes, certain afferent and efferent *visceral* components also pass through the dorsal and ventral nerves. The former are in connection with ganglion cells of the sympathetic system, situated more peripherally, and pass along the dorsal roots; while the latter arise from nerve-cells in the ventro-lateral regions of the spinal cord, and pass out through both the dorsal and ventral roots, without, however, having any physiological connection with the ganglia of the former. These supply the muscles of the viscera and blood-vessels which originate from the lateral plates of the mesoderm (p. 9), but do not innervate the skeletal muscles.

The common *nerve-trunk* formed by the junction of the two roots divides up again into a *dorsal* and a *ventral* branch, containing both afferent and efferent somatic fibres, and a *visceral branch*, containing afferent and efferent visceral fibres. The first of these goes to the muscles and skin of the back, the second supplies the lateral and ventral portions of the body-wall, while the visceral branch supplies the viscera and is in connection with the sympathetic.

1. SPINAL NERVES.

As a general rule, each corresponding pair of dorsal and ventral nerves or nerve-roots lies in the same transverse plane : an exception to this is seen, however, in Cyclostomes, Elasmobranchs, and Dipnoans, in which each ventral pair alternates with a dorsal pair.[1] In Ganoids also, lateral displacements of the nerve-roots are met with.

In Fishes the greatest variations are seen as regards the mode of exit of the nerves, which pass through the intercalary pieces of the vertebral column, or between the arches ; but from Amphibians onwards the nerves always make their exit on either side between the arches, through the intervertebral foramina.

In their primitive undifferentiated condition the spinal nerves have a strictly metameric arrangement, and are equally developed all along the body. In the region of the developing extremities, the nerves bifurcate and extend into the limb, each forming a dorsal extensor and a ventral flexor. This primary condition becomes complicated by the fact that the extensions of the myotomes into the limbs do not all become differentiated simply into a dorsal and a ventral portion, and thus it becomes impossible to draw a hard and fast line between the dorsal and ventral branches of the nerves of the extremities. As a rule, a number of the ventral branches of the spinal nerves in the region of the appendages become connected together to form *plexuses* which, according to their position, are spoken of as *cervical, brachial, lumbar,* and *sacral* (Figs. 145 and 147). The number of nerves composing these corresponds to the number of body-segments taking part in the formation of the appendages, and their relative size is usually directly proportional to the development of the latter. A further important factor in the formation of the limb-plexuses can be traced to the ontogenetic and phylogenetic shifting of the extremities along the trunk, whereby they assimilate nerves from other segments and lose some of those which primarily belonged to them.

In contrast to Fishes, the great variation in the comparatively slightly developed plexuses of which renders it impossible to reduce them to a common plan, we find from the Amphibia onwards a typical grouping of the branches of the *cervico-brachial* and *lumbo-*

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[1] In Amphioxus, the dorsal and ventral nerves alternate right and left, so that a right dorsal and a left ventral nerve are in the same transverse plane and *vice versâ*, and the fibres composing the ventral nerves are not surrounded by a common sheath. The dorsal nerves of Amphioxus and Petromyzon, like many of the cerebral nerves of all Craniata, are throughout of a mixed nature, and this was possibly the case in the Protovertebrata.

sacral plexuses, in which dorsal and ventral branches can usually be recognised.

In the brachial plexus, which from the Sauropsida onwards is more sharply differentiated from the cervical plexus, the following may be distinguished: (1) anterior (superior) thoracic nerves (*dorsalis scapulæ* and *thoracicus lateralis* of human anatomy); (2) posterior (inferior) thoracic nerves (*subclavius, thoracici anteriores*); (3) ventral (anterior) brachial nerves (*medianus*, with the *musculo-cutaneus, ulnaris,* and *cutaneus medius* et *internus*); (4) dorsal (posterior) brachial nerves (*subscapulares, axillaris,* and *radialis*).

The lumbo-sacral plexus shows in general, and more particularly in Mammals, much greater variations than does the brachial plexus. The nerves arising from it are also arranged in a dorsal and a ventral series, the larger ones being spoken of as the *obturator*, *crural*, *sciatic*, and *pudendic*. The sciatic divides up in the hind-limb into a *tibial* and a *fibular* nerve. The numerous individual variations seen in the lumbo-sacral plexus (*e.g.* of Man) are due to the fact that the pelvic girdle has not yet acquired such a fixed position with regard to the trunk as has the shoulder-girdle, and shows a tendency to become shifted forwards.[1]

2. CEREBRAL NERVES.

It is customary to distinguish the following twelve pairs of cerebral nerves, and of these the eleventh have a distinct origin only in the Amniota, and the twelfth are represented by the anterior spinal nerves in certain Fishes and in all Amphibians:—

I. Olfactory.
II. Optic.
III. Oculomotor.
IV. Pathetic or trochlear.
V. Trigeminal.
VI. Abducent.
VII. Facial.
VIII. Auditory.
IX. Glossopharyngeal.
X. Vagus or pneumogastric.
XI. Spinal accessory.
XII. Hypoglossal, in close connection with which are certain "spino-occipital" nerves.

Of these, the purely sensory olfactory and optic nerves have an isolated position as regards their mode of development from the secondary and primary fore-brain respectively, and they are dealt with in the sections on the brain and the olfactory and optic organs.

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[1] In animals in which the extremities have disappeared, all traces of the corresponding plexuses have also usually vanished: Snakes, however, still retain remnants of them.

The auditory is also a purely sensory nerve.

The oculomotor, pathetic and abducent supply the muscles of the eye, and probably, like the spinal accessory and hypoglossal, consist exclusively of somatic motor fibres. All the other cerebral nerves, like the spinal nerves, are mixed, and contain, in different proportions, somatic afferent (general cutaneous) and efferent, and also visceral afferent and efferent components.

In their mode of origin the cerebral nerves (except I and II) resemble the spinal nerves in many respects (p. 232), and a gradual transition between the two groups is indicated in the lower Vertebrata. Certain of them, like the motor portions of the spinal nerves, arise as direct outgrowths from the extension of the ventral horns of the spinal cord into the embryonic brain (III, VI, XII, and probably IV).[1]

Others again (V and VII in part, VIII, IX, and X) arise in the embryo from the dorso-lateral region of the brain, and thus resemble the dorsal roots of the spinal nerves, but differ from these (except in the cases of Amphioxus and Petromyzon) in being developed opposite to and not between the corresponding somites: later on their origin becomes shifted to the ventral side of the brain. In all these (except VIII) the visceral system predominates over the somatic owing to visceral muscles occupying the place of somatic muscles. They further resemble the dorsal roots of the spinal nerves in arising from a neural ridge; this, however, is not continuous with that of the spinal cord, which ends in the auditory region, but is more dorsal in position and extends into the trunk-region for a short distance. But in the course of development these two ridges become no longer distinguishable from one another, and complications arise owing to a kind of struggle between the two for mastery, in which the cerebral neural ridge gains the upper hand; thus the rudiments of the spinal ganglia in this region, together with the corresponding somites, become reduced to mere vestiges, the development of the nerves of the visceral arches excluding that of the spinal nerves.

From the cerebral neural ridge certain ganglia arise, viz., the *Gasserian* (V), the *geniculate* (VII), the *petrosal* (IX), and the *jugular* (X); and, as in the case of the spinal ganglia, afferent (sensory) fibres are formed which grow into the brain and are there connected with their cerebral centres. In the formation of these mixed cerebral nerves (and also of the VIIIth), certain ganglionic zones of proliferation of the external ectodermal epithelium

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[1] The fourth nerve is peculiar in appearing from the dorsal surface of the brain, but this is probably a secondary condition. Originally, this and the third nerve possibly belonged to the trigeminal, the sixth to the facial, and all three nerves of the eye-muscles perhaps represent vestiges of primitive cerebral nerves of a mixed nature, as is indicated by the fact that some few sensory fibres may be present in the fourth, and probably the sixth, amongst the Anamnia.

(*placodes*) take part, in addition to the main ganglia already referred to. Two rows of these accessory ganglia (which probably correspond to the vestiges of primitive integumentary sense-organs) may often be distinguished in the embryo in either side of the head—a dorso-lateral, and a more ventral row just above the gill-clefts: the former are spoken of as the *lateral ganglia*, and the latter as the *ventral* or *epibranchial ganglia*, which are associated with transitory epibranchial sense-organs. In their primitive superficial position the two rows are connected with one another and with the central organ by cellular cords.

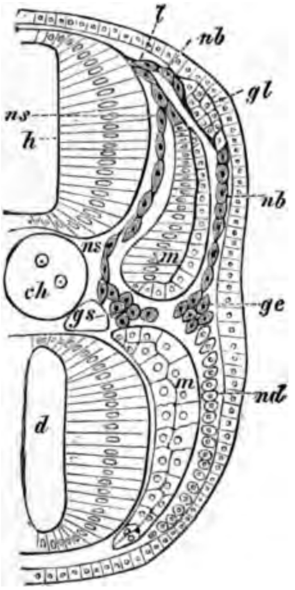

FIG. 178.—DIAGRAM TO SHOW THE MODE OF DEVELOPMENT OF THE DORSAL CEREBRAL NERVES AND THEIR GANGLIA IN THE LAMPREY. (After C. v. Kupffer.)

ch, notochord; *d*, gut; *ge*, epibranchial ganglion (ventral placode); *gl*, lateral vagus ganglion (lateral placode); *gs*, sympathetic ganglion; *h*, hind-brain; *l*, neural ridge (rudiment of the spinal ganglion proper); *m*, mesoderm; *nb*, branchial nerve: *nd*, subepidermoid layer, derived from the ectoderm, and giving rise to the peripheral part of the branchial nerve; *ns*, dorsal spinal nerve.

It is probable that the motor fibres of these mixed nerves (as well as the cerebral portion of XI) grow out secondarily from the brain into the primary ganglionic nerve-rudiments arising from the upper row of nerve-centres formed by the bifurcation of the band-like spinal motor tract. From the ventral row, which lies in the same plane as the ventral horns of gray matter, arise the IIIrd, IVth, VIth, and XIIth nerves, as already mentioned.[1]

It must be remembered that the head is primitively composed of a series of metameres (p. 75), and it is therefore important to ascertain, as far as is possible in the present state of our knowledge, to which individual metameres the different cerebral nerves belong. As already mentioned, the olfactory and optic nerves present certain peculiarities which bring them under another category, and they will be treated of later in connection with the corresponding sensory organs.

The following general summary gives a scheme of the probable primitive relations of the head-segments and cerebral nerves, founded mainly on the conditions existing in Elasmobranch embryos.

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[1] An additional pair of vestigial cerebral nerves has been shown to exist in Protopterus, Ceratodus, Anura, and many Elasmobranchs, arising in the region of the lamina terminalis, crossing the olfactory lobes, and ending in the region of the olfactory mucous membrane. Along the course of this nerve, the function of which is unknown and which has been described as the "nervus terminalis," are one or two ganglia.

TABLE SHOWING THE SEGMENTAL ARRANGEMENT OF THE CEREBRAL NERVES, WITH THEIR RELATION TO THE METAMERES OF THE HEAD.

	Ventral branch.	Dorsal branch.
1st *Metamere* (superior, inferior, and anterior rectus, and inferior oblique muscle).	Oculomotor (*III*).	Ramus ophthalmicus profundus of the trigeminal (*V*), together with the ciliary ganglion.
2nd *Metamere* (superior oblique).	Pathetic (*IV*).	Trigeminal (with its ganglion, *minus* the ramus ophthalmicus profundus).
3rd *Metamere* (posterior rectus).	Abducent (*VI*).	Facial (*VII*), and auditory (*VIII*), with their ganglia.
4th *Metamere* (muscles which are early aborted).	Wanting.	
5th *Metamere* (muscles which are early aborted).	Wanting.	Glossopharyngeal (*IX*), with its ganglion.

Nerves of the Eye-muscles.—The oculomotor (III) pathetic or trochlear (IV) and abducent (VI) nerves (Figs. 179—181) supply the muscles which move the bulb of the eye (cf. table above).

The **oculomotor** arises from the base of the mid-brain, and is in intimate relation with an oculomotor or *ciliary* ganglion which primarily belongs to the sympathetic system, and from which oculomotor fibres pass out to the iris and ciliary muscles of the eye.[1]

The **pathetic** nerve,[2] although actually arising in the interior of the ventral part of the mid-brain, near the nucleus of the oculomotor, appears externally on the dorsal side of the anterior margin of the hind-brain (valve of Vieussens, p. 203).

The **abducent** nerve arises far back on the ventral side of the medulla oblongata: in addition to the posterior rectus, it supplies the retractor bulbi and the muscles of the nictitating membrane in the Sauropsida. In the Anura it becomes intimately connected with the Gasserian ganglion of the trigeminal.

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[1] Further researches are desirable with regard to the ciliary ganglion of Anamnia and Sauropsida. It appears to be made up of two distinct ganglia (cerebro-spinal and sympathetic), one of which, in Mammals, fuses with the Gasserian ganglion during development, the other remaining as the ciliary ganglion of the adult.

[2] Before emerging on the roof of the brain, the fibres of each trochlear nerve cross those of its fellow (*chiasma trochleare*), so that the right nerve supplies the left superior oblique muscle, and *vice versa*. Originally this muscle may be a derivative of muscles which once supplied the parietal eye.

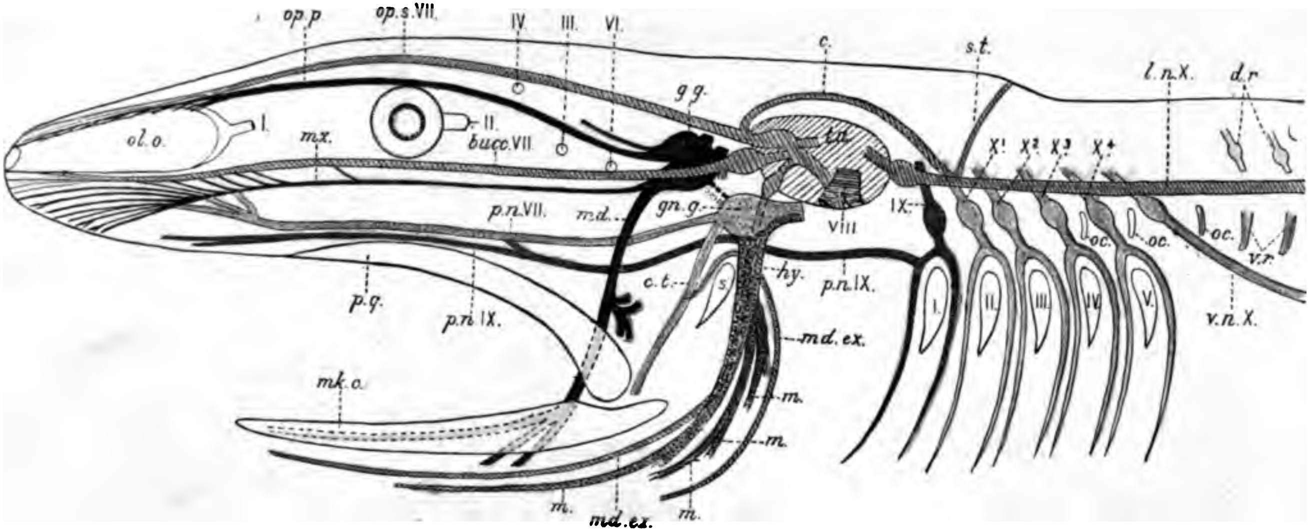

FIG. 179.—DIAGRAM SHOWING THE PRINCIPAL BRANCHES OF THE CEREBRAL NERVES IN A FISH. (Slightly modified by Bridge.)

mk.c, Meckel's cartilage ; *ol.o*, olfactory organ ; *p.q*, palatoquadrate ; *s*, spiracle ; *I-V*, branchial clefts ; *I*, *II*, *III*, *IV*, *VI*, the first, second, third, fourth, and sixth cerebral nerves. The remaining nerves are differently shaded.

Black.—The trigeminal (Vth nerve). *g.g*, Gasserian ganglion ; *m.d*, mandibularis ; *mx*, maxillaris ; *op.p*, ophthalmicus profundus.

Oblique shading.—The lateralis system and its centre (*t.a*), the tuber acusticum. *bucc. VII*, buccalis branch of VII ; *md.ex*, external mandibular branch of VII ; *l.n.X*, lateralis nerve, with its supra-temporal branch (*s.t*), and its commissural connection (*c*) with *op.s. VII*, ophthalmicus superficialis of *VII* ; *VIII*, auditory nerve.

Dotted.—The facialis proper, *VII*, including *c.t*, chorda tympani ; *gn.g*, geniculate ganglion ; *hy*, hyomandibularis, with its motor branches, *m*, *m*, *m* ; *p.n. VII*, palatine.

Dark gray.—The glossopharyngeal (*IX*), with its pre- and post-branchial branches and its palatine nerve (*p.n.IX*), anastomosing with the palatine branch of VII (Jacobson's anastomosis).

White.—The vagus : X^{1-4}, the branchial nerves, ganglionated and forking over clefts *II-V* ; *v.n.X*, visceral nerve ; *oc*, spino-occipital nerves. *d.r* and *v.r*, the dorsal and ventral roots of the first two spinal nerves. (For the ganglia belonging to the sympathetic system, cf. Fig. 180.)

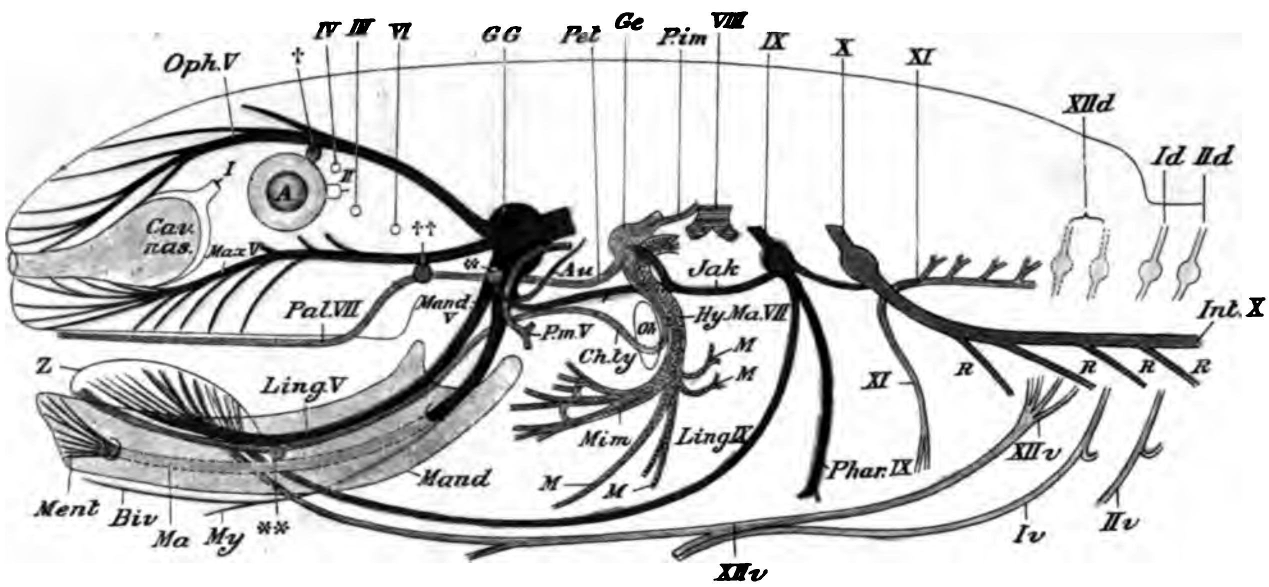

FIG. 180.—DIAGRAM SHOWING THE DISTRIBUTION OF THE CEREBRAL NERVES IN THE AMNIOTA.

Car.nas, olfactory organ; *A*, eye; *Oh*, tympano-eustachian passage; *Mand*, mandible; *Z*, tongue.

I, olfactory nerve; *II*, optic nerve; *III*, oculomotor nerve; *IV*, pathetic (trochlear) nerve; *VI*, abducent nerve. The other nerves are distinguished by different kinds of shading, to correspond with Fig. 179, except that *IX* is shaded black.

V, trigeminal, with its three branches; the ophthalmic (*Oph.V*), maxillary (*Max.V*), and mandibular (*Mand.V*), the last-named dividing into a mandibular in the narrower sense (*Ma*), and a lingual (*Ling.V*). The latter is connected with a motor portion (*P.m.V*) and with the chorda tympani branch of the facial (*Ch.ty*); *Ment*, branches to chin; *Biv*, *My*, motor branches which supply the ventral belly of the biventer and the mylohyoid muscles; *Au*, auriculo-temporal branch.

VII, facial; *Ge*, geniculate ganglion; *Pet*, major superficial petrosal nerve, which arises from the sensory portion of the facial, and extends forwards beyond the spheno-palatine ganglion (††) as the palatine (*Pal.VII*); *Ch.ty*, chorda tympani, part of which in Mammals extends through the middle ear (*Oh*); *Hy.Ma.VII.*, main (hyomandibular) trunk, which in Primates gives rise to the plexus (*Mim*) for the facial muscles; *M*, *M*, branches to the muscles of the ear and to the visceral muscles; *P.im*, intermediate portion of facial.

VIII, auditory nerve.

IX, glossopharyngeal. *Ling.IX*, lingual, and *Phar.IX*, pharyngeal branch; *Jak*, anastomosis of Jacobson, connecting the glossopharyngeal and facial nerves.

X, vagus. *Int.X*, intestinal branch, with its further subdivisions, *R*, *R*, *R*, *R*.

XI, spinal accessory.

XIIv, hypoglossal; *XIId*, its vestigial dorsal roots.

Id, *IId*, and *Iv*, *IIv*, dorsal and ventral roots of the first two spinal nerves.

Ganglia derived from the sympathetic. †, ciliary; ††, sphenopalatine, which is connected with the facial by the superficial petrosal nerve; *, otic, connected with the facial and glossopharyngeal by the anastomosis of Jacobson; **, ubmaxillary, perforated by the chorda tympani nerve.

The trigeminal, facial, glossopharyngeal, and vagus nerves are usually described as *branchial* or *branchiomeric* nerves, *i.e.* they are primarily related to gill-clefts. A typical branchial nerve has a ganglion near its origin from the brain and divides into (1) a *dorsal* (somatic sensory) branch to the skin, (2) a *palatine* (visceral sensory) branch to the oral mucous membrane, and (3) a branch associated with the epibranchial ganglion (p. 236) which bifurcates over the corresponding branchial cleft into a *prebranchial* (visceral sensory) and a *postbranchial* (visceral motor) nerve.

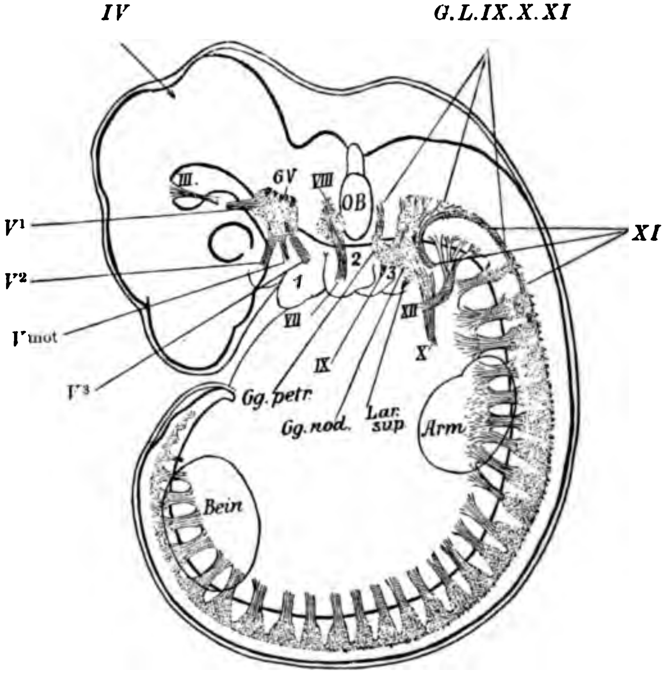

FIG. 181.—PERIPHERAL NERVES OF A HUMAN EMBRYO OF 4 WEEKS (6·99 MM. IN LENGTH), RECONSTRUCTED FROM SECTIONS. (After G. S. Streeter.)

1, 2, 3, mandibular, hyoid, and 1st branchial ridges; *III*, oculomotor; *IV*, trochlear; *V*^{1}, *V*^{2}, *V*^{3}, the three main branches of the trigeminal; *V*mot, motor portion of trigeminal; *G V*, ganglion of trigeminal; *VII*, facial; *VIII*, auditory ganglion; *IX*, glossopharyngeal with the petrosal ganglion (*Gg.petr*); *X*, vagus with the ganglion nodosum (*Gg.nod*) and the anterior (superior) laryngeal nerve (*Lar.sup*); *G.L*, ganglionic ridge of the *IXth*, *Xth*, and *XIth* nerves; *XII*, hypoglossal. The abducent (VI) is not visible.

Trigeminal Nerve.—This is one of the largest of the cerebral nerves. It arises from the ventro-lateral region of the anterior part of the medulla oblongata (pons Varolii of Mammals) by a large sensory and a smaller (ventral) motor root, has a large primarily double intra-cranial or extra-cranial *Gasserian ganglion* at the origin of the former, and in Fishes (Fig. 179), divides into two main branches, an *ophthalmic* (including a *superficial* and a *deep* or *profundus* portion), and a *maxillo-mandibular*: in most terrestrial forms (Figs. 180 and 181) the maxillary and mandibular nerves arise separately. From the presence of these three characteristic branches, often known as the *first*, *second*, and *third divisions* of the trigeminal, its name is derived. It passes out from the skull sometimes through a single aperture, and sometimes by two or three distinct ones. On the supposition that the mouth corresponds to a fused pair of branchial clefts, the ophthalmic would correspond to the dorsal branch of a branchial nerve, and the maxillary and mandibular to the prebranchial and postbranchial branches; the palatine branch may be represented by a branch going to the roof of the mouth.

The superficial branch of the first division is usually distinct in Fishes, in many of which, however, and in higher forms, it may be united with the deep branch. In Amphibians its homology has not been clearly made out.[1] It passes dorsally over the eye-ball, crosses the superficial ophthalmic branch of the facial, with which it may become secondarily connected, and is distributed to the skin anterior to and above the orbits. The deep branch passes below the superior and anterior recti and superior oblique muscles, and supplies the integument of the snout, the eyelids and conjunctiva, the mucous membrane of the nose, and the lacrymal glands (*e.g.* in Mammals). A connection of the profundus with the ciliary ganglion arises secondarily.

The second division of the trigeminal, like the superficial and deep ophthalmic, is purely sensory. On it is a *sphenopalatine ganglion* derived from the sympathetic, and it is connected with the facial. It extends first along the floor of the orbit, supplying the lacrymal and Harderian glands when present, the conjunctiva, the mucous membrane of the nose, and the roof of the mouth; it then passes to the upper jaw, supplying the teeth; and finally, as the infraorbital branch, perforates the skull to reach the integument in the region of the upper jaw, snout, and upper lip.

The third division of the trigeminal is of a mixed nature; its motor portion, which has the character of a visceral nerve, supplies certain masticatory muscles and some of the muscles of the palate and floor of the mouth. The sensory portion extends along the rami of the lower jaw and divides into two main parts, a *lingual* and a *mandibular proper*, the former of which is not well differentiated in the Anamnia and Sauropsida. The lingual or gustatory nerve innervates the mucous membrane of the mouth and tongue, containing gustatory fibres from the chorda tympana (cf. under facial nerve).

The special mandibular branch, which may pass through the inferior dental canal of the mandible, supplies the teeth and mucous membrane of the lower jaw, and then gives off one or more branches to the integument of the latter and of the lower lip: in Mammals, a smaller branch passes upwards in front of the ear to the temporal region, supplying the adjacent skin and the pinna of the ear. Two ganglia, the *submaxillary* and the *otic* (Fig. 180), derived from the sympathetic, are connected with its sensory portion, the former being situated close beneath the exit of the nerve from the skull, the latter on the lingual nerve at the point where it passes into the tongue. The otic ganglion is connected with the glossopharyngeal nerve, but it is doubtful whether the gustatory fibres in connection with the lingual ganglion are derived from this nerve or from the facial.

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[1] It possibly corresponds to the ramus frontalis of Mammals.

Facial Nerve.—This, which is also a mixed nerve, presents important differences in branchiate and pulmonate forms respectively. In many Fishes (*e.g.* Cyclostomes, Elasmobranchs, many Teleosts, Dipnoans) and in perennibranchiate Urodeles, it possesses two distinct ganglia at its origin in connection with the sensory and mixed portions respectively. In other Fishes (*e.g.* Chimæra, Polypterus, Lepidosteus, certain Teleosts) and more especially in Anurans, the facial nerve comes into such close connection with the trigeminal that the ganglia in question are no longer distinguishable from the Gasserian ganglion, and such complications arise that the original relations of many of the components of the two nerves are no longer traceable and cannot be analysed by dissection. Another (the *geniculate*) ganglion of the facial nerve is retained in all Vertebrates.

In aquatic branchiate Vertebrates the facial nerve consists of the following main branches (Fig. 179):

I. A system of sensory branches for the supply of the integumentary sense-organs of the head (*q.v.*). These branches, together with the auditory nerve and the lateral line branches of the glossopharyngeal and vagus (p. 245), arise from the same centre in the medulla oblongata (*tuber acusticum*), each originally possessing its own ganglion, and together forming a primitive acustico-lateral sensory nervous system, arising, like the sensory organs which they supply, direct from the ectoderm. The following branches may be distinguished:—(*a*) a *superficial ophthalmic*, running parallel to the like-named branch of the trigeminal and sometimes (*e.g.* in Chimæra) becoming very closely connected with its deep portion; (*b*) a *buccal*, close to the maxillary portion of the trigeminal, and, giving off near its origin an *otic* branch; and (*c*) an *external mandibular*, in the region of the hyomandibular nerve, dividing into an anterior and a posterior branch and frequently anastomosing with the mandibular branch of the trigeminal.

II.—A sensory (*a*) *palatine*,[1] which may anastomose with the maxillary branch of the trigeminal and which innervates the mucous membrane of the pharynx, and (*b*) *chorda tympani*,[1] going to the mucous membrane of the floor of the pharynx. These two nerves correspond to the "portio intermedia" of the facial of Mammals (Fig. 182), and are closely related at their origin with the geniculate ganglion. The chorda tympani corresponds to the prebranchial and the hyomandibular to the postbranchial branch, but from Amphibians onwards the chorda tympani becomes post-spiracular in position.

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[1] There can be no doubt that the palatine branch of the facial in the Anamnia, comparable to the visceral or pharyngeal branches of the glossopharyngeal and vagus, corresponds to the greater superficial petrosal of Mammals, which is a purely sensory nerve: the motor fibres which are said to arise from it probably belong to the vagus.

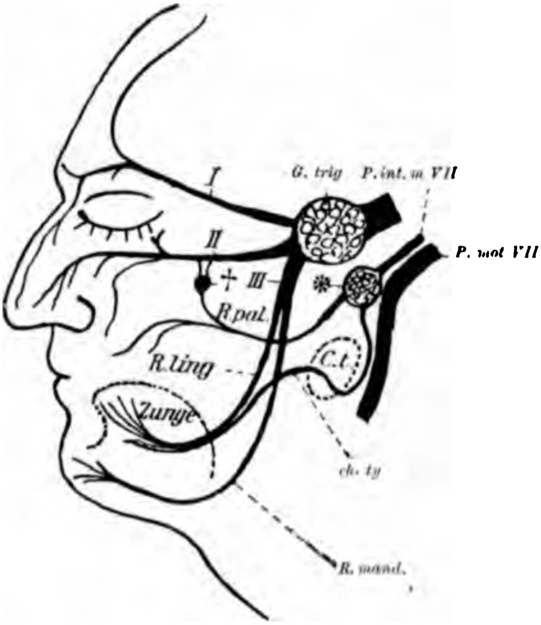

FIG. 182.—DIAGRAM SHOWING THE RELATIONS OF THE PORTIO INTERMEDIA OF THE FACIAL NERVE IN MAN. (After A. F. Dixon ; slightly modified.)

I, *II*, *III*, the three branches of the trigeminal ; *, geniculate ganglion of the facial ; †, sphenopalatine ganglion, in the neighbourhood of *II* ; *Ch.ty*, chorda tympani ; *C.t*, tympanic cavity, outlined ; *G. trig*, Gasserian ganglion of the trigeminal ; *P.int.mVII*, intermediate (sensory) portion of the facial ; *P.mot.VII*, motor portion of the facial (hyomandibular) ; *R.ling*, lingual branch of *III* ; *R.mand*, mandibular branch of *III* ; *R.pal*, palatine (greater superficial petrosal) branch of facial. The motor portion of trigeminal *III* is not indicated.

III. A main post-spiracular *hyomandibular* trunk, extending along the hyoid arch, and essentially motor, except for the components which give rise to the sensory external mandibular and a few twigs supplying the mucous membrane of the spiracle, anterior wall of the pharynx, floor of the mouth, and the skin. Its motor fibres supply visceral muscles in connection with the mandibular and hyoid arches.

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[1] The chorda tympani ("alveolar" branch of the facial) passes internally to the lower jaw in Elasmobranchii, Ganoidei, Perennibranchiata, and Anura. In other Amphibians, as in Reptiles, it passes into the bony lower jaw.

In correspondence with the change from an aquatic to a terrestrial mode of life, the integumentary sense-organs in caducibranchiate Urodela, Anura, and in Amniota, become more or less completely lost, and the corresponding branches of the facial nerve are reduced. The parts which persist, in addition to the large motor hyomandibular, are the palatine and the chorda tympani (cf. Figs. 179–182).

In the Amniota the chorda tympani has a very different position from that seen in the Anamnia, and becomes characteristically related to the tympanic cavity; in Birds it is absent, and is replaced functionally by the glossopharyngeal. From the Amphibia and Reptilia onwards, a gradual development of the facial muscles leads to the characteristic mimetic muscles of Mammals and more especially of Primates, which are supplied by the hyomandibular nerve. The complicated networks of this nerve, however, appears late phylogenetically, and are wanting even in certain embryonic stages in Man. In addition to the mimetic muscles, the hyomandibular nerve in Mammals supplies the platysma, the stylohyoid, the posterior belly of the digastic, and the stapedius.

Auditory Nerve.—This large nerve, which has a ganglion at its origin, arises in close connection with the facial, and comes under the same category as the sensory portion of the latter nerve, inasmuch as it is probable that the auditory organ is a modified portion of the lateral line organs. Soon after its origin it divides into a *vestibular* and a *cochlear* branch. The latter passes to the lagena or cochlea of the ear, while the former supplies the rest of the auditory labyrinth.

Vagus group.—This group includes the glossopharyngeal, vagus, and spinal accessory, which stand in the closest relation to one another, and, owing to the fact that the head in this region has undergone fewer phylogenetic modifications, are less specialised than the cerebral nerves already described. These nerves all consist of both afferent and efferent fibres, the former being connected with ganglia (the *petrosal* of IX, and the *jugular* and *cervical* of X).

In Fishes and perennibranchiate Amphibians the **glossopharyngeal** leaves the skull through a special foramen, and not along with the vagus, as in other Vertebrates. In branchiate forms, in addition to a palatine branch, it is distributed to the region of the first (hyobranchial) gill-cleft, over which it bifurcates into a smaller prebranchial and a larger postbranchial branch (Fig. 179). In other Vertebrates it is distributed to the pharynx and tongue, and as a rule anastomoses with the vagus and also with the geniculate ganglion or palatine branch of the facial and the otic ganglion of the third division of the trigeminal (*Jacobson's anastomosis*), a continuation of this branch extending forwards, close to the palatine branch of the facial.[1] In the higher Vertebrates, the large lingual branch forms a gustatory nerve supplying the tongue, tonsils, and epiglottis: this nerve is apparently already indicated in Dipnoans.

The **vagus** has a very wide distribution, and is not limited to the head but extends into the trunk. It includes a sensory lateral line branch, pharyngeal (=palatine), and branchial branches; the last-mentioned fork over the second and following gill-clefts and supply the mucous membrane and muscles of the branchial apparatus in branchiate forms. Its visceral branch supplies the larynx, heart, swim-bladder or lungs, and a considerable portion of the digestive tract (gullet, stomach, and more or less of the intestine). In pulmonate Vertebrates a reduction takes place of the motor components of the branchial nerves along with the corresponding muscles (Fig. 180).

The origin of both glossopharyngeal and vagus by numerous roots, and the fact that they give off branches in the region of the pharynx and visceral arches in which a metameric arrangement can be recognised, indicates that they correspond originally to a number of separate nerves.

The lateral branch of the vagus, as already mentioned (p. 242), does not belong originally to this nerve, but to the lateral nervous system of the head, having a similar central origin to that of the acustico-facial group, with which it may even be directly connected by a commissure outside the auditory capsule (Protopterus). There is a special ganglion at its origin from the medulla (Fig. 179), and its exit from the skull by the same foramen as the vagus is evidently secondary. After giving off a supratemporal branch, it extends along the trunk to the apex of the tail, and may subdivide into several branches, some of which may be situated directly under the skin and others (like the main lateral nerve of Elasmobranchs and Dipnoans), beneath the lateral muscles close to the vertebral column. All these branches supply the sensory organs belonging to the lateral line system.[2]

The so-called **spinal accessory** (*accessorius Willisii*) is a true cerebral nerve, and can already be recognised in Elasmobranchs, in which it is included in the vagus, from the posterior roots of which it arises: it is therefore primitively a cerebral and not a spinal nerve. It presents certain characteristic peculiarities in the Amphibia, Sauropsida, and Mammalia respectively, so that a direct comparison of the nerve in these groups is impossible.[1]

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[1] It is possible that the lateral line fibres which may be associated with the glossopharyngeal, and even with the trigeminal, are always derived from the vagus and facial.

[2] Certain nerves present in Teleostomes and formerly described under the term "ramus lateralis trigemini," may be included under the term "*ramus lateralis accessorius*." They form a sensory system of nerves, provided with ganglia, which are formed typically from somatic sensory fibres derived from the Vth, VIIth, IXth, and Xth cerebral nerves and a varied number of spinal nerves. Branches pass to some of, or even all, the fins, and supply sensory end-buds (*q.v.*). The so-called lateral nerve of Petromyzon belongs to this system.

Owing to secondary differentiations, the accessory of Mammals takes on a very different character from that of the Sauropsida: only that part of it in the former arising from the spinal cord can properly be described as the accessory, while its cerebral portion must be included under the vagus group. In the Sauropsida, the nerve is better described as the spinal portion of the vagus. In Mammals, the accessory contains viscero-motor elements from the dorsal roots of the 5th to 7th spinal nerves, and extending along the course of the vagus gives off branches to the larynx and to the trapezius and sternocleidomastoid muscles.

Spino-occipital and Hypoglossal Nerves.—Under the term "spino-occipital nerves" is understood a group of nerve-roots in the occipital region and anterior trunk-myotomes which are in close relation to the hypoglossal. As most of their components are bound up in the vagus-group, they were formerly erroneously described as "ventral roots of the vagus."

In Cyclostomes they have either not been assimilated by the cranium (cf. p. 85) or are not even differentiated from the cerebral nerves, so that in this case they cannot be spoken of as spino-occipital. In Plagiostomes, in which, as in Amphibians, vertebral elements are fused with the occipital region of the skull, a series of intracranial spinal nerves can be recognised which may be described as "occipital," a reduction in which, from before backwards, can already be observed. In the Holocephali, owing to a still greater assimilation of vertebral elements to the skull, three additional spinal nerves later became intracranial, while the number of occipital nerves is reduced to two.[2] The relative number of these two series varies in Ganoidei, Dipnoi, and Amniota, the occipital nerves having entirely disappeared in the Teleostei.

In Fishes the first spinal nerve, which corresponds to the hypoglossal of higher forms, supplies the muscles of the trunk, the floor of the mouth, and the skin of the back, and also sends twigs to the brachial plexus. In higher Vertebrates the hypoglossal becomes gradually more differentiated from the other cervical nerves, and innervates the intrinsic muscles of the tongue, takes up cervical elements, and with them gives rise to the so-called *ramus descendens* and the *ansa hypoglossi*, from which arise branches to the sterno-hyoid and other muscles.

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[1] The evolution of the spinal accessory in the higher Vertebrates must have taken place somewhat as follows. Beginning with the Amphibia, in which the vagus group does not extend into the spinal cord, the accessory in the primitive Amniota must have possessed the following characters:—close connection with the vagus, extension backwards at least as far as the first cervical segment, origin from a lateral collection of cells of the ventral cornu, and course on the ventral side of the dorsal cornu of the gray substance. From this primitive form the nerve must have developed along two different lines in the Sauropsida and Mammalia respectively, in both of which, however, in contrast to the Amphibia, it thus forms a kind of connecting link between the cerebral and the spinal nerves, this region including in the Sauropsida at most three, in Mammalia seven, segments.

[2] These additional nerves have been described as "occipito-spinal" to distinguish them from the "occipital" nerves: each series constitutes a sub-section of the spino-occipital group. In Amphibians (except Ichthyophis) the occipital nerves are no longer recognisable, even in the embryo.

In the Gymnophiona, Urodela, and Aglossa amongst the Anura, the first spinal nerve perforates the first vertebra: in other Anurans this nerve has disappeared, though occasionally recognisable in the embryo, and the nerve which arises behind the vagus and emerges between the first and second vertebræ in reality corresponds to the second spinal nerve (hypoglossal, cf. Figs. 145 and 164).

From the Sauropsida onwards, the hypoglossal, which arises postero-ventrally to the vago-accessory group, leaves the skull through one or more apertures: it has three roots,[1] which correspond to three spino-occipital nerves of the Anamnia.

Dorsal roots may be present temporarily or permanently in connection with the hypoglossal of Sauropsida and Mammalia, and may be provided with ganglia, as in the case of the accessory and of the spino-occipital nerves of many Fishes. A reduction of dorsal roots may also take place further backwards: in many Mammals, including Man, that of the first cervical nerve (and even of the second in *e.g.* the Orang) may be reduced or entirely wanting.

Sympathetic.

The *sympathetic system* is a derivative of the spinal system, with which it remains throughout life in close connection by means of *rami communicantes* (Fig. 145). It is distributed mainly to the alimentary tract, the vascular system, and the glandular organs of the body.

The sympathetic *ganglia* are derived from the developing spinal ganglia, and, like these, show originally a segmental arrangement. They contain typical ganglion-cells,[2] and usually become united together secondarily by longitudinal *commissures*, thus giving rise to a chain-like paired *sympathetic cord* lying on either side of the vertebral column and aorta. From its ganglia nerves pass off to the above-mentioned organs, and form plexuses. Numerous peripheral ganglia, derived from the others, are also present in the plexuses.

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[1] Other, more anterior elements occur in the embryo in Sauropsida.

[2] A special small form of cell occurs in the embryonic sympathetic ganglia, and may extend beyond them to a greater or less degree into other parts. Thus these *chromaffin cells* are found, *e.g.*, in the pancreas (islets of Langerhans), coccygeal gland, hypophysis (Fig. 151), and suprarenals (medullary substance, *q.v.*):—in fact, in all "glands with internal secretion."

The sympathetic, accompanying the arterial trunks, extends along the vertebral column and passes anteriorly into the skull, where it comes into relation with a series of the cerebral nerves (cf. pp. 237, 241 and Fig. 180) similar to those which it forms further back with the spinal nerves.

The original segmental character frequently disappears later on, and this is especially the case in those regions where marked modifications of the earlier metameric arrangement of the body have taken place—viz., in the neck and certain regions of the trunk, especially towards the tail: thus in Mammals there are never more than three cervical ganglia.

Nothing is known of a sympathetic in Amphioxus. In *Petromyzon* typical ganglion-cells occur more or less sparsely along the dorsal and ventral spinal nerves in the lateral walls of the body. Nests of cells are present more frequently in the region where the parietal veins open into the cardinal veins than alongside the aorta, and they also occur along the caudal vein and its branches: these ganglia are connected with the suprarenal organ (*q.v.*). The sympathetic extends into the head.

In *Elasmobranchs* the sympathetic reaches a higher stage of development, and it has been shown that the ganglia first appear after the dorsal and ventral roots have united to form the spinal nerve-trunks, just at their point of union, each ganglion containing from the first both afferent and efferent elements. Except in its most anterior embryonic segment, in which the ciliary ganglion represents a part of this system, the head is without sympathetic ganglia. A sympathetic cord, connecting the ganglia, is not developed in Elasmobranchs, although some of the individual ganglia may become united together, while others disappear at an early stage.

A cranial portion of the sympathetic exists in *Teleosts,* arising from the trigemino-facial system of nerves and possessing three ganglia: in the trunk, too, there is a well-developed cord of ganglia, frequently connected with its fellow by transverse commissures, the two cords gradually converging antero-posteriorly. A similar condition has been found to occur in the *Dipnoi* (Protopterus), in which the delicate longitudinal sympathetic cords, with occasional ganglia, extend along the aorta and notochord: nothing is known of their connection with the cerebral nerves.

In *Amphibians* (Fig. 145), the sympathetic reaches a high stage of development. It ends anteriorly in the ciliary ganglion, extends along the aorta through the trunk and caudal regions as a ganglionated cord, and has numerous anastomoses with the spinal and cerebral nerves; it is intimately related with the suprarenal and abdominal veins (postcaval and revehent renal veins).

In the *Sauropsida* the cervical portion of the sympathetic is usually double, one part running within the vertebrarterial canal alongside the vertebral artery. In all other Vertebrates the whole cord lies along the ventral and lateral region of the vertebral column: it is generally situated close to the latter, overlying the vertebral end of the ribs.

In *Mammals*, the cervical portion of the cord may have an independent course from the vagus, or it may be more or less closely applied to the latter nerve, the anterior cervical ganglion of the sympathetic and the vagus-ganglion forming a single mass; the posterior cervical ganglion commonly fuses with the first thoracic. From the anterior cervical ganglion the sympathetic passes into the skull along with the internal carotid artery, and its cranial portion takes on relations to the cerebral nerves—more particularly the Vth, IXth, and Xth, as in other Vertebrates. Numerous branches also pass from the anterior cervical ganglion to the hypoglossal, the anterior cervical nerves, and to the pharynx, larynx, &c.

III. SENSORY ORGANS.

The specific elements of the sensory organs originate, like the nervous system in general, from the ectoderm; the peripheral terminations of the sensory nerves are thus always to be found in relation with cells of ectodermic origin, which become secondarily connected by means of nerve-fibres with the central nervous system.[1]

The sensory apparatus was primarily situated on a level with the epiderm, and served to receive sensory impressions of but slightly specialised kinds; but in the course of phylogeny parts of it passed inwards beneath the epiderm, certain of these becoming differentiated into organs of a higher physiological order, viz., those connected with *smell, sight, hearing*, and *taste*. These are situated in the head, and except the last mentioned, become enclosed in definite mesodermic sense-capsules (p. 77); they must be distinguished from the simpler ***integumentary sense-organs***, which are concerned with the senses of *touch, pressure*, and *temperature*. In addition to ***free nerve-endings*** in the skin, various specific forms of ***sensory cells*** occur, and these may be surrounded by ***supporting*** or ***isolating cells***, both kinds, however, being ectodermic. The mesoderm may also take part in the formation of the sensory organs, giving rise not only to the above-mentioned sense-capsules, but also to various protective coverings and canals as well as to contractile and nutritive elements (muscles, blood- and lymph-channels).

In the sensory organs of the integument of branchiate Vertebrates, as well as in all the higher sensory organs, the surrounding medium is always moist, and in both cases, rod-, club-, or pear-shaped sensory cells are met with.

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[1] The vertebrate eye forms an exception to the other sense-organs in that it arises from a part of the ectoderm which has been involuted to form the medullary tube.

In those animals which in the course of development give up an aquatic life and come on land (most Amphibians), the external layers of the epiderm dry up, and the integumentary sense-organs pass further inwards from the surface, undergoing at the same time changes of form. Thus from Reptiles onwards other kinds of sense-organs are met with in the skin.

Sense-Organs of the Integument.

a. Nerve-eminences.

In Amphioxus certain rod-shaped or pear-shaped cells can be recognised in the epiderm, especially in the anterior part of the animal; each of these is provided distally with a hair-like process and proximally is in connection with a nerve. The cells are distributed irregularly, but in the neighbourhood of the mouth and cirri they form groups.

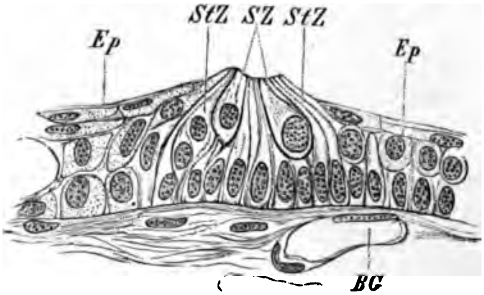

Fig. 183.—Vertical Section through the Skin and a Lateral Line Organ of the Larva of *Triton tæniatus*, 3 cm. in Length. (After F. Maurer.)

BG, blood-vessel; *Ep*, epiderm; *SZ*, sensory cells; *St.Z*, supporting cells.

It is doubtful whether these structures in Amphioxus are directly comparable to the integumentary sense-organs of Fishes and Amphibians, but it is important to note that each of the latter always arises in the first instance from a single cell which forms a group by division. These organs always consist of central cells, arranged in the form of a rounded and depressed pyramid, and of a peripheral mass grouped around the former like a mantle. The central cells are surrounded by a network of nerve-fibres; each of them bears at its free end a stiff cuticular hair, and they are the sensory cells proper: the others have merely an isolating, supporting and slime-secreting function (Figs. 183 and 184).

In Dipnoi, perennibranchiate Amphibia, and amphibian larvæ these organs retain their peripheral free position, on a level with

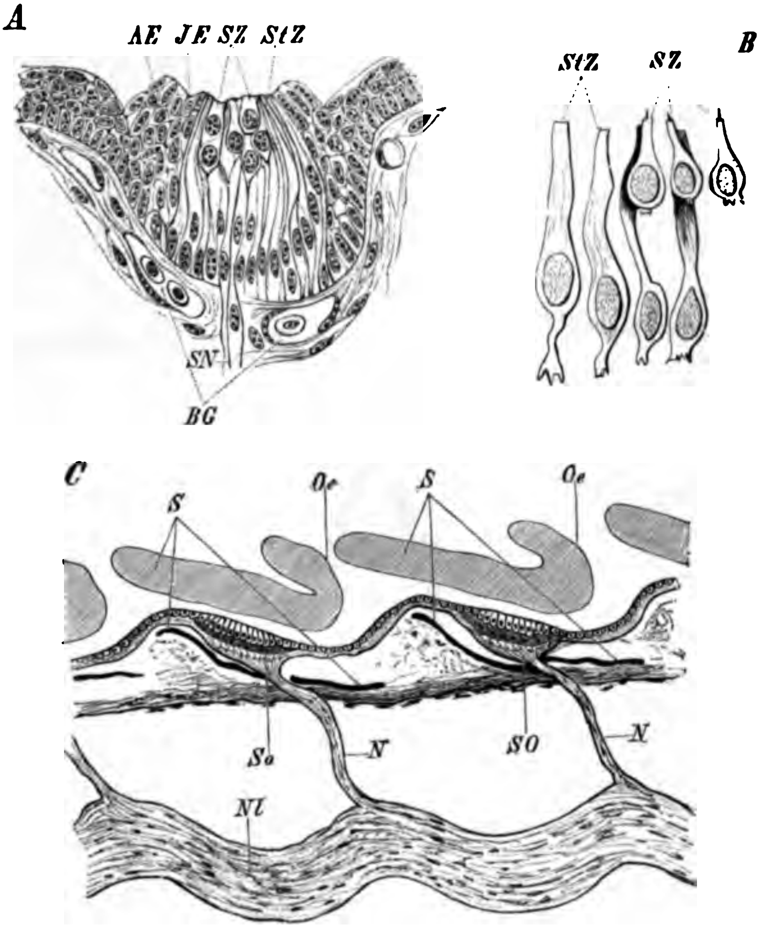

FIG. 184, A.—LONGITUDINAL VERTICAL SECTION OF THE SKIN AND A LATERAL LINE ORGAN OF *Triton cristatus* DURING THE BREEDING SEASON, WHEN THE ANIMAL LIVES IN THE WATER. (After Maurer.)

AE and *JE*, external and internal layers of epiderm abutting against the sensory organs; *BG*, blood-vessel; *SN*, nerve; *SZ*, sensory cells; *StZ*, supporting cells.

B.—ISOLATED SUPPORTING (*StZ*) AND SENSORY (*SZ*) CELLS FROM A LATERAL LINE ORGAN OF TRITON.

C.—VERTICAL SECTION THROUGH THE LATERAL CANAL OF *Amia calva*. (After Allis; slightly modified.)

Nl, lateral nerve, and *N*, branches to sensory organs; *Oe*, apertures of the lateral canal to the exterior; *S*, scales; *SO*, sensory organs in the lateral canal.

the epiderm,[1] but in other Fishes (as is also the case on the head in Dipnoans) they may eventually become enclosed in depressions or complete canals: these are often branched, and are formed either by the epiderm only, or more usually, by the scales and bones of the head, and they open externally from point to point (Fig. 184, C).

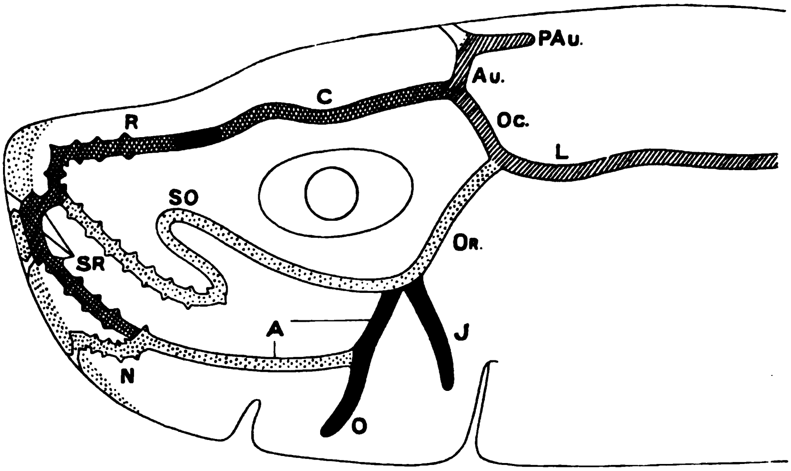

FIG. 185.—SENSORY CANALS OF *Chimæra monstrosa*. (After F. J. Cole.) The innervation is indicated by the different kinds of shading.

(1.)—Supra-orbital canal (innervated by superficial ophthalmic of facial—cross-hatched: the black segment is the portion innervated by the profundus) = cranial (*C*) + rostral (*R*) + sub-rostral (*SR*).
(2.) Infra-orbital canal (buccal + otic of facial—dotted) = orbital (*Or*) + sub-orbital (*SO*) + portion of angular (*A*) + nasal (*N*).
(3.) Hyomandibular or operculo-mandibular canal (external mandibular of facial—black) = remainder of angular (*A*) + oral (*O*) + jugular (*J*).
(4.) Lateral canal (lateral line branch of vagus—oblique shading) = lateral (*L*) + occipital (*Oc*) + aural (*Au*) + post-aural (*PAu*).
The small dots on the snout represent the apertures of ampullary tubes.

The distribution of these sensory organs extends over the whole body, but (except, *e.g.* in Petromyzon), they are situated characteristically along certain tracts, the position of which is very constant: on the head, *supra-orbital*, *infra-orbital*, and *hyomandibular* tracts

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[1] At the time when an Amphibian undergoes metamorphosis and gives up its aquatic habits, these sensory organs sink downwards into the deeper layer of the skin, and, as the epiderm grows together over them, they become shut off from the exterior and reduced, and may finally disappear (Anura and certain Caducibranchiata). In others of the latter group, in which they are retained and also new ones are formed, they come to the surface when the animal returns to the water during the breeding season (Fig. 184, A). Peculiar sense-organs are present in the aquatic Xenopus and in Ichthyophis glutinosus. The horny wart-like structures arising periodically during the breeding season in Cyprinoids, and known as "pearl-organs," are due to a modification of the reduced nerve-eminences. Similar structures occur in Anura.

can be recognised, and along the sides of the body and tail are one or more *lateral lines*[1] (Figs. 185 and 186). These structures are thus often spoken of as *segmental sensory organs*, or *organs of the lateral line*[2]: primarily they have not a metameric arrangement, and where such is seen, it is always secondary. The portions lying in the region of the head are the first to be developed. They are innervated by the lateral line branches of the facial, glossopharyngeal and vagus (cf. pp. 242, 245).

It is thus clear that the entire lateral nervous system and its modifications, including the auditory organ, is a specialised system differing morphologically and histologically from all the other integumentary sense-organs.

The so-called *Savi's vesicles* of Torpedo, the *nerve-sacs* or *pit-organs* of Teleostomes, and the *ampullary tubes* of Elasmobranchs correspond to modified nerve-eminences. These are all limited in their distribution to the head and anterior portion of the trunk, being most numerous on the snout: they arise from thickenings of the epiderm which later become invaginated and in which a sensory epithelium is differentiated. In Teleostomes these organs retain a simple sac-like form, and are situated abundantly on the head and along accessory lateral lines on the trunk: in Torpedo they become completely separated from the epiderm, while in other Elasmobranchs they are tubular, each tube giving rise to one or more swellings or ampullæ of varied form enclosing radial folds of connective tissue and containing the nerve-end organs, which are supplied by the lateral-line system of nerves. The tubes are filled with a gelatinous substance.

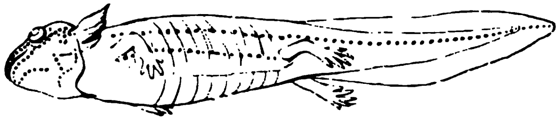

FIG. 186.—DISTRIBUTION OF THE LATERAL SENSE-ORGANS IN A SALAMANDER LARVA.

These integumentary sense-organs are extremely ancient structures, for traces of them have been observed in Jurassic Elasmobranchs, and even in the Devonian Cephalaspidæ and

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[1] There are several lateral lines in Polypterus and various other Fishes, in Proteus, and in all amphibian larvæ.

[2] The lateral canal system of Polyodon comes nearest to that of Elasmobranchs, and in Acipenser it shows certain resemblance to that of Bony Ganoids; in that the sensory organs become embedded within cranial elements. In Lepidosteus, branched secondary canals arising from the main canals of the head extend into the cranial bones: this is not the case in Polypterus. In Teleosteans the system is very different from that of Elasmobranchs, but resembles that of Ganoids in many respects—*e.g.* in often having the canals protected by [illegible] structures: in other respects the different families and species differ much [illegible] one another, and reductions of the lateral line organs [illegible] Siluroids).

Pteraspidæ: the so-called "spectacles" of Archegosaurus probably belong to the same category. Their function is not thoroughly understood, but there is no doubt that they are concerned with the perception of mechanical stimuli from the surrounding water, and are thus probably important in appreciating the direction of these stimuli. As already mentioned (p. 242), they and the auditory organ are genetically related to one another, the ear being merely a specialised portion of the lateral line system.

b. End-buds and gustatory organs.

Although various intermediate forms between the nerve-eminences and end-buds occur, it is an open question as to whether there is any genetic connection between these two kinds of sense-organs, and it is important to bear in mind that the nerve-supply in the two cases is a very different one.

In contrast to the nerve-eminences, which tend to sink below the surface, the end-buds usually form a dome-like elevation projecting above the general level of the epiderm. A central sensory epithelium, provided with sensory hairs, and peripheral supporting cells can be recognised, but the former are as long as the latter. These organs are supplied by the facial nerve.

In Lampreys and most Elasmobranchs they remain at a primitive stage of development, but become of great importance in Teleostomes, in which they are scattered irregularly over the whole body and are particularly numerous on the fins, lip-folds, barbules, and mouth.

From Dipnoans onwards they are limited to the oral, pharyngeal, and nasal cavities, and are supplied by the IXth and Xth as well as by the VIIth nerve. Thus in Amphibians they occur on the papillæ of the oral and pharyngeal mucous membrane, on the margins of the jaws, and on the apices of the fungiform papillæ of the tongue, which may possibly have a gustatory function.

In Reptiles the distribution of these organs is somewhat more limited, and in Birds true taste-buds, though present in the mouth and pharynx, are wanting on the horny tongue. The lingual branch of the glossopharyngeal nerve is, however, strongly developed in many groups (*e.g.* Lamellirostres), and functionally replaces the sensory branch of the trigeminal, which is wanting in the avian tongue.[1]

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[1] In Lizards and Crocodiles typical gustatory organs are present, chiefly on the soft, glandular mucous membrane of the pharynx: they are wanting on the tongue and in the anterior part of the oral cavity. In Birds their distribution is apparently dependent on the size and form of the tongue: when the latter is narrow, they are situated on the thin, glandular mucous membrane of the lower beak; and when it is broad, on that of the upper beak or of the pharynx. Their arrangement is irregular, and their number varies greatly in the different groups, being greatest in Parrots (300–400), in which their structure resembles that of the gustatory organs of Mammals.

In Mammals, organs of taste are still found on the soft palate, on the walls of the pharynx, and even extend into the larynx; but they are most numerous on the tongue, where they occur on the circumvallate and fungiform papillæ as well as on the papilla foliata.[1]

Thus the specific integumentary sense-organs of aquatic Vertebrates have not entirely disappeared in terrestrial forms, certain of these (end-buds) being retained even in Mammals, under the necessary condition of a moist medium.[2]

c. *Tactile cells and corpuscles.*

(Terminal ganglion-cells.)

In these structures there is no longer any direct connection with the surface of the epiderm, and supporting cells are wanting.

"Tactile spots," consisting of groups of tactile cells, are met with for the first time in tailless Amphibians, in which they are usually situated on small elevations, and are distributed over the skin of the whole body (Fig. 187, A). Phylogenetically they are probably derivable from the integumentary sense-organs of the Ichthyopsida. In Reptiles, amongst which they retain the simplest form in Hatteria and are arranged along the margins of the scales, they are found chiefly on the lips and sides of the face and on the snout, but in some cases (as in Blindworms, Snakes, and young Crocodiles) they are present on the scales over the whole body, and are usually arranged symmetrically. In Snakes and Birds the tactile cells are confined to the mouth-cavity (tongue) and to the beak (cere), and are much closer together, forming definite masses, or tactile corpuscles. Each of these is surrounded by a nucleated connective tissue investment from which septa extend into the interior, partially separating the individual tactile cells from one another: the "Grandry's corpuscles" occurring on the beak (Fig. 187, D) are modified tactile corpuscles.

In Mammals the tactile cells are either isolated—as, for instance, on the hairless portions of the body, or they give rise to oval corpuscles, each consisting of a many-layered and nucleated investment, into which a nerve passes, becomes twisted up, and comes into relation with one or more terminal cells (Fig. 187, B, C). These are most numerous and highly developed on the volar and plantar

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[1] Two circumvallate papillæ are present in Monotremes, three in Marsupials, and a variable number in the Eutheria. Foliate papillæ are especially well developed in Rodents, but in many Mammals are little marked or wanting. The relative functional importance of the different kinds of papillæ varies in the course of the individual life in Man. In Cetaceans (*e.g.* Dolphin) only vestiges of the gustatory organs are retained.

[2] Nothing is known as to whether certain of these organs in lower Vertebrates are concerned with the sense of taste, or whether a change of function has taken place in passing to the higher forms: the nerve-supply is, however, interesting.

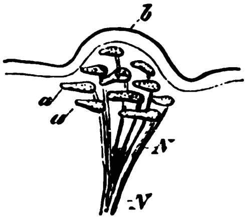

FIG. 187A.—A TACTILE SPOT FROM THE SKIN OF THE FROG. Semi-diagrammatic. (Modified from Merkel.)

a, *a*, neuro-epithelium; *b*, epiderm; *N*, nerve, which loses its medullary sheath at N^1.

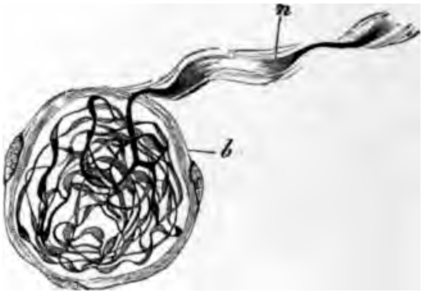

FIG. 187C.—A TACTILE CORPUSCLE (END-BULB, OR KRAUSE'S CORPUSCLE) FROM THE MARGIN OF THE CONJUNCTIVA OF MAN. (After Dogiel.)

b, nucleated fibrous investment; *n*, medullated nerve fibre, the axis-fibre of which passes into a closely coiled terminal skein.

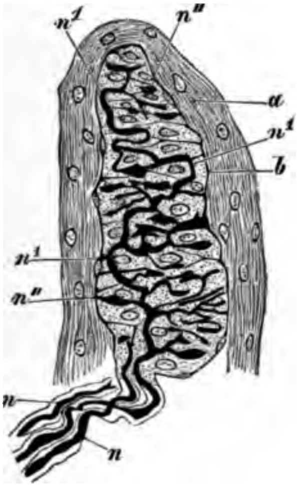

FIG. 187B.—DERMAL PAPILLA FROM THE HUMAN FINGER ENCLOSING A TACTILE CORPUSCLE (MEISSNER'S CORPUSCLE). (After Lawdowski.)

a, fibrous and cellular investment; *b*, tactile corpuscle, with its cells; *n*, nerve-fibre; *n'*, the further course of the nerve-fibre, showing its curving branches; *n''*, terminal twigs of the nerve-fibres with club-shaped endings.

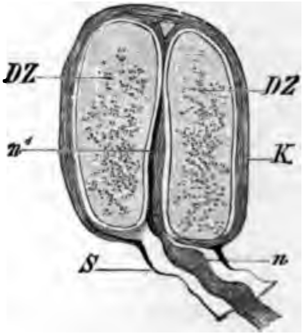

FIG. 187D.—TRANSVERSE SECTION THROUGH A TACTILE CORPUSCLE (GRANDRYS' CORPUSCLE) FROM THE BEAK OF A DUCK. (After Carrière.)

n, nerve, entering the capsule *K*, its sheath (*S*) becoming continuous with the latter. The nerve passes between the two covering-cells, *DZ*, *DZ*, widening out to form a tactile plate at n^1.

surfaces of the hand and foot respectively and on the conjunctiva and snout, and are especially well-marked on the snout in the Mole:

they are simplest on the glans penis and glans clitoridis. It is doubtful whether they occur on hairy portions of the skin, though it is certain that the hairs (and more especially the vibrissæ, cf. p. 30), have a sensory function, which is very marked in the case of those on the wings and ears of Bats.

Circumscribed and well-innervated areas, each composed of a cap of thickened and curiously modified epithelium covering a dermal papilla, have been observed in numerous Mammals close to the hairs: these *hair-discs* represent a special kind of sensory apparatus. In Man, each disc is a small, rounded structure situated in the acute angle between the oblique hair-shaft and the skin-surface: in a corresponding position in the obtuse angle opposite to it is another well-marked, smooth area, probably corresponding to a scale-rudiment. These two structures, together with the other accessory organs of the hair (glands, muscles, nerves, vessels, &c.), constitute a well-defined "*hair-area*," which is probably the morphological equivalent of the reptilian scale.

d. Club-shaped or lamellar corpuscles.

(Pacinian corpuscles.)

In Lizards and Snakes club-shaped corpuscles are present in addition to the above-described tactile organs, occurring chiefly in the region of the lips and teeth and also on the body (*e.g.* Lacerta); they have an elongated, oval form, and their structure is simple.

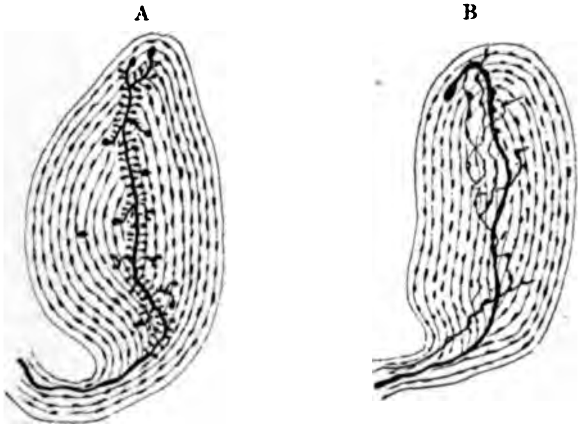

FIG. 188.—PACINIAN CORPUSCLE FROM MESORECTUM OF KITTEN—A, two days, and B, three days old. (After Guido Sala.)

In A the nerve-network is seen surrounding the main fibre. In B, knob-like outgrowths are shown on the fibre at its distal end.

When more highly developed, the interior of each corpuscle shows the continuation of the axis-fibre of the nerve surrounded by numerous lamellæ: on it either knob-like buds or networks can be recognised, the latter surrounding the main fibre (Fig. 188). Often also there is a double column of cells surrounding the axis.

Organs of this kind are universally present in the deeper layers of the derm in Birds and Mammals: in the former they are particularly abundant on the beak and at the bases of the contour-feathers of the wings and tail, and are also found on the tongue. They occur, moreover, in various other regions, both in Birds and Mammals (*e.g.* on the various organs of the abdominal cavity, the conjunctiva, the fasciæ, tendons, ligaments, the vas deferens, periosteum, submaxillary glands, mesentery, pericardium, pleura, corpus cavernosum and spongiosum, the wing-membrane of Bats, &c.). Their size varies greatly even in the same individual.

The tactile cells and tactile and club-shaped corpuscles are all concerned with the sense of touch and pressure. It is impossible to say definitely what nerve-endings have to do with the perception of temperature; it is not improbable that the touch-cells, as well as the nerve-fibres often provided with varicose swellings which end freely in the epiderm, are here concerned. Such *free nerve-endings* occur in the skin of all Craniata and consist of a branched, intercellular network, no direct connection between nerve and epithelial cell having been observed.

OLFACTORY ORGAN.

The olfactory nerves are connected with the olfactory lobes which arise as prolongations of the secondary fore-brain, the ventricle of which is temporarily or permanently continued into them: as already mentioned, each olfactory lobe is, in some cases, differentiated into bulb, tract, and tubercle.

The filaments of the olfactory nerves are arranged in a single bundle on either side, or in two more or less distinct bundles. The individual fibres pass from the cranial cavity into the nasal cavity either separately, through a cribriform plate of the ethmoid (p. 129), or through a single aperture on either side. The latter is the case, *e.g.* in Fishes, all Amphibians except Menopoma, Reptiles, all Birds except Apteryx and the extinct Dinornis, and Ornithorhynchus: in all Mammals except the last mentioned a cribriform plate is present.

The primary origin of the olfactory organ is by no means understood, and it is doubtful whether it can be said to have a true olfactory function in aquatic types. In its simplest form, the organ consists of a ventral, paired, pit-like depression of the integument of the snout opening on to the surface by an external nostril. It is lined by ectodermal epithelium, which gives rise to a "primary olfactory ganglion," the individual elements of which at first resemble unipolar nerve-cells: from these, the olfactory fibres grow centripetally towards the olfactory lobes and pass into the fore-brain, when they become connected with the olfactory centre. The individual olfactory cell and fibre thus form an organic unit—a primitive condition such as occurs in certain integumentary sense-organs of Worms and Molluscs, but not in any of the other sensory cells of Vertebrates. The olfactory cells thus constitute the only true *neuro-epithelium* in Vertebrates, as the nerve arises in connection with the cell itself, with which it remains continuous (*primary sensory cell*): in other *secondary* nerve-cells, the relation of cell and nerve is one of apposition merely.

In their final form, the olfactory cells are elongated, swollen in the region of the nucleus, and bear hair-like processes on their free ends, while proximally each is continuous with a nerve-fibre (Fig. 189). Between them are isolating or supporting cells, which have a similar origin, and ciliated cells may also be present.

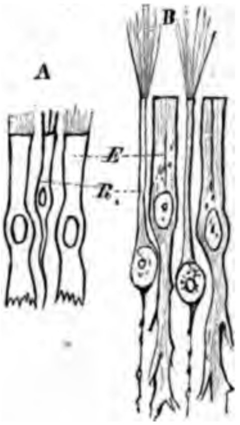

FIG. 189.—EPITHELIUM OF THE OLFACTORY MUCOUS MEMBRANE. A, of *Petromyzon planeri*; B, of *Salamandra atra*.

E, interstitial epithelial cells; *R*, olfactory cells.

The olfactory organs in all Fishes are of a simple sac-like form, but from the Dipnoi onwards they come to communicate with the cavity of the mouth as well as with the exterior. In consequence of this, *anterior* or *external nostrils*, and *posterior* or *internal nostrils* (*choanæ*) can be distinguished: as a free passage is thus formed through which air can pass, the olfactory organ takes on an important relation to the respiratory apparatus, and in it olfactory and respiratory regions can be distinguished.[1] From the Amphibia onwards glandular elements are present, the secretion of which serves to keep the nasal cavity moist.

In **Amphioxus,** the ciliated pit supplied by a nerve and situated above the anterior end of the central nervous system probably represents an unpaired olfactory organ.

Cyclostomes.—In these forms the olfactory organ consists of a sac enclosed by a fibro-cartilaginous capsule containing numerous radial folds of the mucous membrane enclosing tun-shaped sense-buds, and is unique in being *unpaired* (Fig. 190). It lies just in front of the cranial cavity, and opens on the *dorsal* surface of the head by a chimney-like tube, which in Myxine is long and is supported by rings of cartilage. This tube is continued backwards from the ventral side of the olfactory organ above the mucous

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[1] The mode of formation of the primitive choanæ is already indicated in many Elasmobranchs as well as in the embryo of Ceratodus, in which a groove, bounded by folds of the skin, extends backwards from each external nostril to the mouth (Fig. 191, A), through which water passes. In Mammals there is no naso-oral funnel, and the development of the choanæ in the higher Vertebrates is accompanied by a secondary perforation of the primarily blind nasal sac.

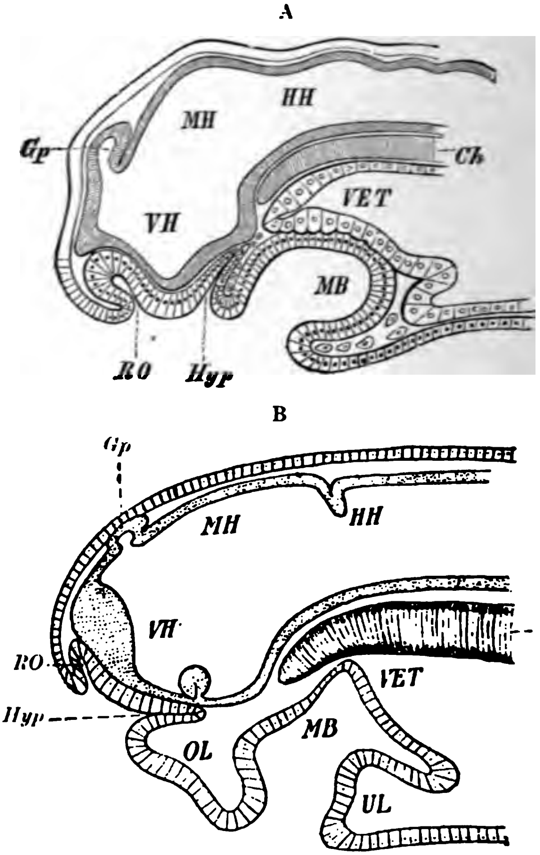

FIG. 190.—A, B, C, MEDIAN LONGITUDINAL SECTION THROUGH THE HEAD OF A LARVA OF *Petromyzon planeri* IN THREE SUCCESSIVE STAGES, TO SHOW THE MODE OF DEVELOPMENT AND RELATIONS OF THE OLFACTORY AND PITUITARY SACS AND THEIR GRADUAL SHIFTING FROM THE VENTRAL TO THE DORSAL SIDE, OWING TO THE GROWTH OF THE ORAL FUNNEL. (Mainly after Kupffer and Dohrn.)

Ch, notochord ; *Chias*, optic chiasma ; *Gp*, pineal body ; *HH*, hind-brain ; *Hyp*, pituitary sac ; *Inf*, infundibulum ; *MB*, stomodæum ; *MH*, mid-brain ; *OL*, *UL*, upper and lower margins of oral funnel ; *RO*, olfactory sac ; *VET*, position of endodermic part of gut shown in C (*VOD*) opening into the stomodæum ; *VH*, fore-brain.

membrane of the mouth : in Petromyzon it forms a blind pouch, but in Myxine opens into the oral cavity as a ***naso-palatine duct.***

Although the olfactory nerve is paired, the first trace of the olfactory sac in the embryo is seen as an unpaired plate, which soon becomes grooved: its unpaired character is probably secondary. In Petromyzon it arises on the ventral side of the head in front of the oral involution (stomodæum), and between it and the mouth is another ectodermal invagination, the *pituitary sac* (Fig. 190). In the course of development the olfactory and pituitary invaginations become sunk in a common pit, which, owing to the growth of the large oral funnel, gradually becomes shifted to the dorsal side. On the further elongation of the naso-pituitary sac to form the above-mentioned tube, the olfactory sac opens into it posteriorly, and is incompletely divided into right and left halves by a septum which grows down from the dorsal side. The pituitary body arises by the formation of follicles from the pituitary sac where it passes below the infundibulum.

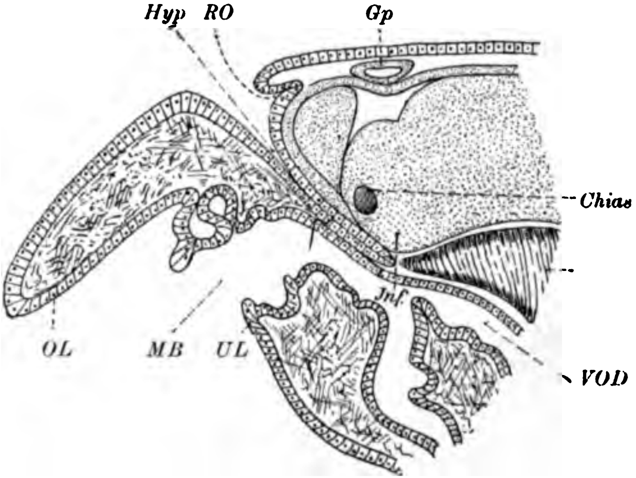

FIG. 190, C.

Fishes.—The position of the olfactory organ in Elasmobranchs (Fig. 191, A) differs from that seen in Cyclostomes in being on the under instead of the upper surface of the snout, and thus retains a more primitive position. In many forms each nostril is connected with the mouth by a naso-oral groove (cf. Note on p. 259). From these Fishes onward the organ is always paired, each sac being more or less completely enclosed within a cartilaginous or bony investment forming an outwork of the skull, and being situated between the eye and the end of the snout, either laterally or more or less dorsally.

In the course of development each external nostril of Teleostomes becomes completely divided into two portions, an anterior and a posterior, by a fold of skin. The anterior aperture is often, and the posterior sometimes, situated at the summit of a longer or shorter tube, lined by ciliated cells, and the distance between the

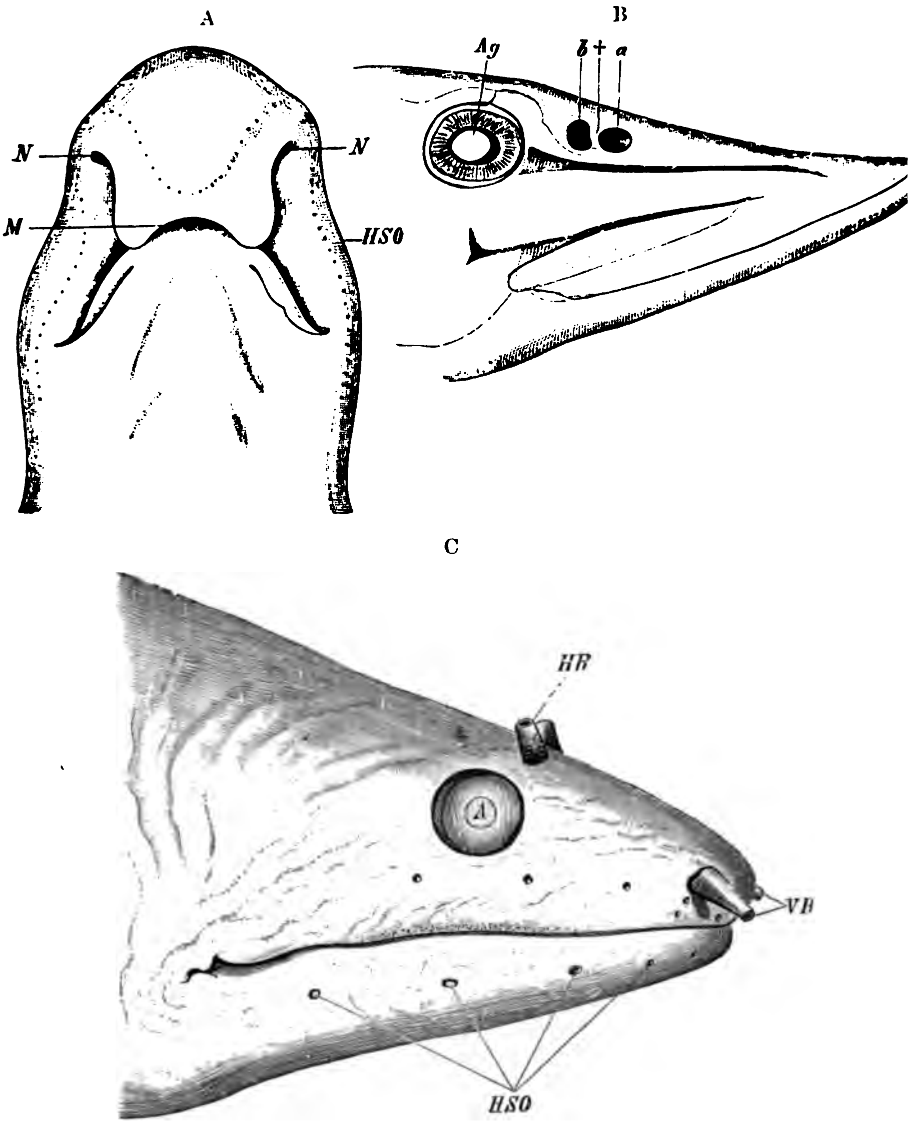

FIG. 191.—*A*, VENTRAL VIEW OF THE HEAD OF A DOGFISH (*Scyllium canicula*). *HSO*, integumentary sense-organs; *M*, mouth; *N*, nostril.

B, LATERAL VIEW OF THE HEAD OF A PIKE (*Esox lucius*). *Ag*, eye; *a* and *b*, the anterior and posterior openings of the external nostrils, and †, fold of skin separating them.

FIG. 191.—*C*, LATERAL VIEW OF THE HEAD OF *Muræna helena*.

A, eye; *HSO*, integumentary sense-organs; *VR* and *HR*, anterior and posterior narial tubes.

two apertures varies greatly, according to the width of the fold of skin which separates them (Fig. 191, B and C). A passage for the water is thus here also present, but, unlike that of Elasmobranchs, is not connected with the mouth.

The mucous membrane of the nasal organ of Fishes is always raised up into a more or less complicated system of folds, which may have a transverse, radial, rosette-like, or longitudinal arrangement, and on which the sensory cells, as well as ciliated cells, are situated.[1]

A nasal skeleton which is well differentiated from the skull proper is met with for the first time in Dipnoans. In Protopterus it consists of a cartilaginous trellis-work, enclosing the olfactory sac and united with its fellow in the median line by a solid septum: the floor is formed mainly by the pterygopalatine and by connective tissue. The mucous membrane is raised into numerous transverse folds connected with a longitudinal fold, and the olfactory organ in general most nearly resembles that of Elasmobranchs, except that, as already mentioned (p. 259), internal as well as external nostrils are present. The latter open beneath the upper lip, and so cannot be seen when the mouth is closed; the former open into the oral cavity rather further back.[2]

Amphibians. — The olfactory organ of Perennibranchiates resembles in many respects that of the Dipnoans: it is always enclosed within a complete or perforated cartilaginous capsule situated laterally to the snout close beneath the skin, and is not protected by the bones of the skull (Fig. 192). Its floor is largely fibrous, and the mucous membrane is raised into radial folds like those of Cyclostomes and Polypterus.

In the higher Amphibia the olfactory organ is more completely included within the cranial skeleton, and its structure becomes modified in correspondence with the change in the mode of respiration, the nasal chamber giving rise to a special respiratory portion, into which the external and internal nostrils open. In Urodeles, the lumen of the organ is from the first simple, while in Anurans, dorsal, middle, and ventral portions may early be distinguished; but in both cases the cavity becomes complicated later by the development of blind pouches or grooves, which are, however, more marked in Anura, and more especially in Gymnophiona, than in Urodela. The prominences or ridges projecting into the nasal lumen between the pouches are analogous to the turbinals of higher forms. A *main* chamber and a more laterally situated *accessory* cavity can be distinguished, the latter extending into the maxillary bone (Fig. 193). In certain Gymnophiona the accessory chamber becomes entirely shut off from the main cavity and receives a special branch of the olfactory nerve, so that in these cases two separate nasal cavities can be distinguished. The external nostrils are always lateral in the adult, but in Urodeles, this position is attained secondarily. They are opened and closed by muscles.

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[1] The olfactory organ probably reaches its highest development and most complicated form amongst Fishes in Polypterus. The nostril leads into an outer cavity, which communicates with the olfactory sac proper, and the latter is divided up into six radial compartments arranged around a central spindle and separated by complicated septa, so that a transverse section of the organ somewhat resembles in appearance that of an orange. In certain representatives of the Plectognathi and Gymnodontes amongst Teleosts, on the other hand, the organ shows various stages of degeneration, and may even undergo almost entire reduction.

[2] The peculiar position of the anterior nares has a physiological significance, at any rate in Protopterus, in connection with the habits of the animal; during its summer sleep the animal breathes through a tube, passing between the lips, formed from the capsule or cocoon which encloses it. The necessary moisture for the olfactory mucous membrane during this time is provided by the numerous goblet cells which line the walls of both nostrils (cf. p. 20).

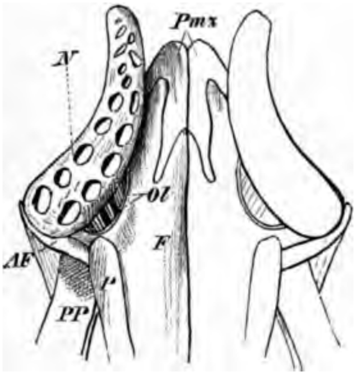

FIG. 192.—OLFACTORY ORGAN OF *Necturus maculatus*. From the dorsal side.

AF, antorbital process; *F*, frontal; *N*, olfactory sac; *Ol*, olfactory nerve; *P*, process of the parietal; *Pmx*, premaxilla; *PP*, palatopterygoid.

Glands, situated under the olfactory mucous membrane, are now met with in terrestrial forms; these are either diffused, or united to form definite masses. They either open directly into the nasal cavity, their secretion serving for the necessary moistening of the mucous membrane (effected in Fishes and in larval and perennibranchiate Amphibians by the external medium), or they pour their secretion into the pharynx or posterior nostrils. The latter are always situated

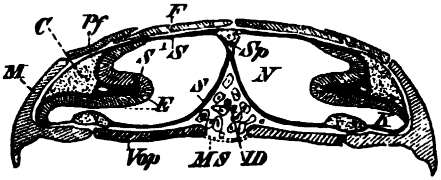

FIG. 193.—TRANSVERSE SECTION THROUGH THE OLFACTORY CAVITIES OF *Plethedon glutinosus*.

C, cartilaginous, and *S*¹, fibrous portion of the turbinal, which causes the olfactory epithelium (*E*) to project far into the nasal cavity; *F*, frontal; *ID*, intermaxillary gland, shut off from the cavity of the mouth by the oral mucous membrane (*MS*), *K*, maxillary cavity; *M*, maxilla; *N*, main nasal cavity; *Pf*, prefrontal; *Sp*, nasal septum; *S*, *S*¹, olfactory mucous membrane; *Vop*, vomero-palatine.

tolerably far forwards on the roof of the mouth, and are for the most part enclosed by the vomer, or vomero-palatine.

A *naso-lacrymal duct* passes out from the anterior angle of the orbit, through the lateral wall of the nose, and opens into the nasal cavity on the inner side of the upper jaw. It conducts the lacrymal secretion from the conjunctival sac of the eye into the nasal cavity, and arises in all Vertebrates, from the Myctodera onwards, as an epithelial cord which is separated off from the epiderm, and, growing down into the derm, becomes hollow secondarily. A naso-lacrymal duct is wanting in Proteus and Siren.

Reptiles.—Owing to the growth of the brain and facial region and to the formation of a secondary palate (p. 112), the olfactory organs, from Reptiles onwards, gradually come to extend more ventrally beneath the cranium. As in Amphibians, a lateral or ventral respiratory, and a median olfactory portion can be recognised.

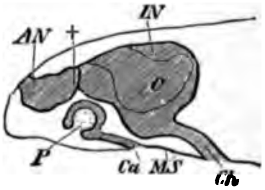

FIG. 194.—DIAGRAM OF THE OLFACTORY ORGAN OF A LIZARD. (Longitudinal vertical section.)

AN, *IN*, outer and inner nasal chambers; +, tube-like connection between them; *Ch*, internal nostrils; *MS*, oral mucous membrane; *P*, papilla of Jacobson's organ (*q.v.*), and *Ca*, its aperture of communication with the mouth.

The simplest olfactory organs amongst Reptiles are seen in Lizards, Snakes, and many Chelonians. The nasal cavity of Lizards, for example, is divided into two portions, a smaller outer (anterior), and a larger inner (posterior) or olfactory chamber proper (Fig. 194). The latter alone is provided with sensory cells, the former being lined by ordinary stratified epithelium continuous with the epiderm: it may contain goblet-cells, but encloses no aggregated glands, and externally to the epithelial layer are muscular elements and cavernous tissue. A large fold or *turbinal*, slightly rolled on itself, arises from the outer wall of the inner nasal chamber, and extends far into its lumen; this is also well developed in Ophidia, in which a distinct outer nasal chamber is wanting, but is very simple in the Amphisbænidæ. The skeletal supports of the turbinals in Reptiles as in all higher forms, are developed secondarily.

A large gland which opens at the boundary between the inner and outer nasal cavities lies within the turbinal (except in Hatteria), and corresponds to the superior nasal gland of Urodeles. Below the turbinal is the aperture of the lacrymal duct: in some Reptiles this opens on the roof of the pharynx (Ascalabota), and in others into the internal nostrils (Ophidia), which, as in Amphibians, are usually situated on the anterior part of the roof of the mouth.

The structure of the nose in Chelonians is very complicated and varied. In marine Chelonians the organ is divided into two passages, one above the other, and connected by means of a perforation of the septum. The comparative paucity of glands in the olfactory organ of Lizards and Snakes forms a marked contrast to the condition seen in Chelonians, the nasal organ of which is characterised by a great abundance of them.

The extension downwards and backwards of the olfactory organ is most marked in Crocodiles, in correspondence with the forward growth of the facial region and the formation of the palate; its posterior part thus lies below the brain and base of the skull, the naso-pharyngeal passage being so much elongated that the posterior nostrils open far backwards into the pharynx. Each nasal chamber is divided posteriorly into two superimposed cavities, the upper of which represents the proper olfactory chamber, and is lined by sensory epithelium, while the lower serves as a respiratory passage only. Certain accessory air-chambers are connected with the nasal cavity. A large gland is present between the olfactory chamber and its investing bones, and opens on either side of the nasal septum, posteriorly to the external nostrils, by one or two apertures. As in other Reptiles, there is only a single true turbinal, but externally to it lies a second prominence, which may be spoken of as a *pseudo-turbinal*, and which possibly corresponds to the upper turbinal of Birds.

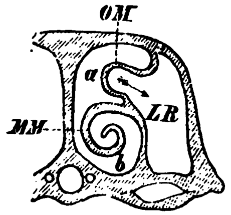

FIG. 195.—TRANSVERSE SECTION THROUGH THE RIGHT NASAL CAVITY OF A SHRIKE (*Lanius minor*).

a, upper, and *b*, lower nasal passage; *LR*, air-chamber, which extends into a hollow of the upper turbinal; *OM*, *MM*, upper and middle turbinals.

Birds.—In all Birds, as in Lizards, there is an outer chamber lined by stratified epithelium, and an olfactory chamber proper, situated above the former. In addition to a turbinal corresponding to that of Reptiles and usually known as the *middle turbinal*, there is a so-called *upper turbinal* (Fig. 195): the former is comparable to the maxillo-turbinal and the latter to the naso-turbinal of Mammals (*q.v.*). A special projection composed of undifferentiated epithelium and situated in the outer chamber may be distinguished as the *vestibular turbinal*. There is no longer any olfactory epithelium on the middle turbinal in the adult, and the upper turbinal during development gradually passes backwards relatively to the middle turbinal, which is usually supported by cartilage or more rarely by bone, and the form of which varies greatly. It may be represented by a moderate-sized prominence, or may become more or less rolled on itself: the lacrymal duct opens below and anteriorly to it. The narrow, slit-like internal nostrils open comparatively far back.

The so-called external nasal gland of Birds is situated on the frontal or nasal bones, along the upper margin of the orbit. It is supplied by the first and second branches of the trigeminal, and corresponds to the lateral nasal gland of Lizards.

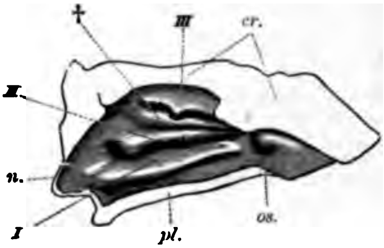

Fig. 196a.—Lateral View of the Nasal Chamber in the Human Embryo.

I, inferior (maxillary), *II*, middle, and *III*, superior turbinal; *cr*, base of skull; *n*, tip of nose; *os*, Eustachian aperture; *pl*, hard palate; †, supernumerary ridge (ectoturbinal) which occurs in the embryo.

Mammals.—Corresponding to the more marked development of the facial portion of the skull, the nasal cavity of Mammals is proportionately much larger than in the forms described above, and consequently there is much more room for the extension of the turbinals. These give rise to a spongy labyrinth, with cell-like compartments lined by mucous membrane; and thus variously-shaped projections, supported partly by cartilage and partly by bone, are seen extending into the nasal cavity, and the olfactory organ reaches its highest development amongst Vertebrates. As in other terrestrial forms, however, a posterior (upper) *olfactory region* of considerable vertical extent, and an anterior (lower) *respiratory region* can be recognised, in each of which turbinals, with their skeletal supports, are developed (Figs. 196–198).

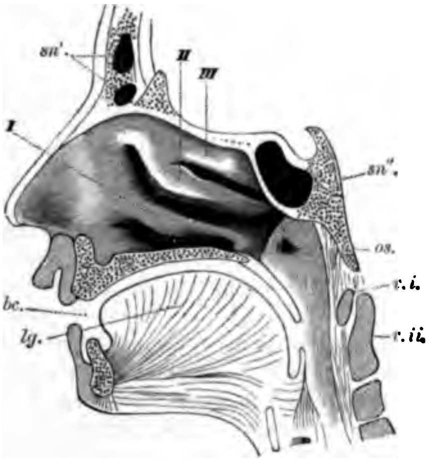

Fig. 196b.—Sagittal Section through the Nasal and Buccal Cavities of the Human Head.

I, inferior (maxillary), *II*, middle, and *III*, superior turbinal; *bc*, entrance to mouth; *lg*, tongue; *os*, aperture of Eustachian tube; *sn'*, frontal sinus; *sn''*, sphenoidal sinus; *v.i*, atlas vertebra; *v.ii*, axis vertebra.

In the olfactory region are found a series of true olfactory ridges, or scrolls, situated in the posterior or median parts of each nasal chamber. The mucous membrane covering these contains olfactory cells and is supplied by the olfactory nerve; their skeletal supports become united later to the ethmoid. In the respiratory portion, which communicates with the pharynx by the posterior nostrils, the turbinals arise from the lateral walls of the chamber and are developed later than the ethmoid turbinals: their skeletal framework unites with the maxillary bone, while a less complicated ridge, which may unite with the nasal bone, can usually be recognised. The *ethmoturbinals* project forwards between the *nasoturbinals* and *maxilloturbinals*; the two last-mentioned no longer possess an olfactory epithelium, and have plainly undergone a change of function in connection with the perception of the warmth and moisture of the inspired air. When well-developed, the maxilloturbinal forms a single or double coil, and may even be more or less branched (Fig. 197); fibres of the maxillary division of the trigeminal supply its mucous membrane.

The ethmoturbinals referred to above (*endoturbinals*) are peculiar to Mammals, as are also certain accessory folds situated laterally to them and also belonging to the ethmoid (Fig. 198): these may be described as the postero-lateral or *ectoturbinals* to distinguish them from the endoturbinals and from the antero-lateral maxilloturbinals and nasoturbinals, which correspond to those of the Sauropsida.

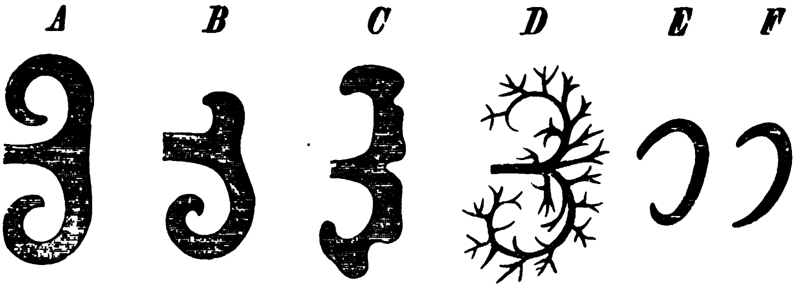

FIG. 197.—VARIOUS FORMS OF THE MAXILLOTURBINAL BONE IN MAMMALS.

A, double coil; *B*, transition from latter to single coil, *E*, *F*; *C*, transition from double coil to the dendritic form D. (After Zuckerkandl.)

The ethmoid turbinals are arranged in a row more or less parallel or obliquely to the palate: their number and relative development varies considerably amongst Mammals and is proportionate to the development of the olfactory lobes and sense of smell. In Monotremes two extreme types are seen: Echidna possesses a highly developed and complicated labyrinth of six or more scrolls, while in Ornithorynchus the labyrinth is greatly reduced in adaptation to an aquatic mode of life. A definite type with five endoturbinals occurs in Marsupials, and this may be taken as primarily typical for the Eutheria: it is approached most nearly in Insectivores, in which there are from four to six, and a very similar condition is seen in Hyrax, Bats, Carnivores, Rodents, and Lemurs. In Ungulates, Elephants, and Edentates, further complications have arisen, and the number of endoturbinals has considerably increased secondarily (*e.g.* to nine in Orycteropus). In Primates (Figs. 196 and 199), on the other hand, reduction has occurred from the condition found in Lemurs.[1]

The ectoturbinals differ so greatly in the individual orders and even species that they cannot be reduced to a common type. In Marsupials, Insectivores, Hyrax and Bats, they are few in number, while in Ungulates, Elephants, Carnivores, Seals, Edentates, Rodents, and in Echidna, they are more numerous: in Ornithorhynchus the ectoturbinals are entirely wanting, as is also the case in most Primates and to a less extent in Lemurs.

According to the degree of development of the olfactory apparatus, taking specially into account its cerebral portion (olfactory lobes, &c., cf. pp. 200, 228), we may distinguish between Mammals which are *macrosmatic* (the majority of the mammalian orders), *microsmatic* (*e.g.* Seals, Whalebone-Whales, Primates), and *anosmatic* (most Toothed Whales).

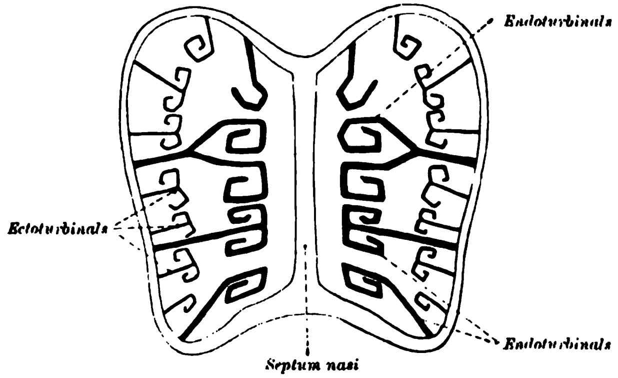

FIG. 198.—DIAGRAMMATIC TRANSVERSE SECTION THROUGH THE NASAL CAVITY OF A MAMMAL, TO SHOW THE RELATIONS OF THE ENDO- AND ECTO-TURBINALS. (Modified from Paulli.)

Except in Monotremes, the nasal chamber communicates with neighbouring cavities, such as the maxillary, frontal, and sphenoidal sinuses (Figs. 196B and 199): the two last-mentioned cavities arise in connection with the nasal apparatus, and in forms with a well-developed sense of smell may enclose olfactory folds;

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[1] Primates possess one to three ethmoturbinals, but traces of as many as five have been recognised in the embryo. The nasoturbinal in anthropoid Apes and Man is also more or less reduced.

In addition to a reduction or entire degeneration of these parts in Cetacea, the nose is shortened and the nostrils have a dorsal position, some distance back from the apex of the snout: in the toothed forms they unite and open by a single valvular aperture. In this Order a series of paired "nasal sacs" are present under the skin, the function of which is not known.

but with the reduction of this sense, they lose their primary function, often persisting merely as air-sinuses or even disappearing entirely[1] (Pinnipedia).

The *nasal glands* of Mammals may be divided into two sets,—numerous small, diffuse *Bowman's* glands, and a large *Stenson's gland*. The latter appears early in the embryo, and in many cases undergoes reduction; it is situated in the lateral or basal walls of the nasal cavity, opening into the vestibule of the nose, and may extend into the maxillary sinus.

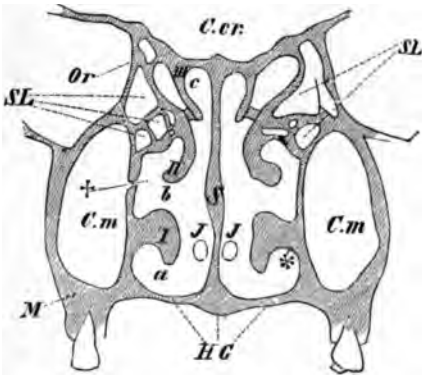

FIG. 199.—TRANSVERSE VERTICAL SECTION THROUGH THE NASAL CAVITY OF MAN.

a, *b*, *c*, inferior, middle, and superior nasal passage; *C.cr*, cranial cavity; *HG*, hard palate; *I*, *II*, *III*, inferior (maxillary), middle, and superior turbinal; *J*, *J*, position of vestigial Jacobson's organs, which are situated nearer the floor of the cavity than is indicated in the figure; *M*, maxilla; *Or*, wall of orbit; *S*, septum nasi; *SL*, ethmoidal labyrinth; *, point at which the nasolacrymal duct opens; †, entrance into the maxillary sinus (*C.m*).

The presence of an *external nose* (cf. p. 131), which must be regarded as a derivative of the outer nasal chamber of Reptiles and Birds, is very characteristic of the olfactory organ of certain Mammals, that of Man being of a specialised type not exactly comparable to the so-called external nose of other Mammals. It is supported by an outward extension of the nasal bones and by the cartilaginous septum nasi which arises from the ethmoid, by the roofing lateral nasal cartilages connected with the septum, and by the vomer, as well as by other secondarily independent cartilages (*alinasals*), which were primarily continuous with the general solid cartilaginous wall, but become differentiated from the latter in various ways in accordance with varied functional adaptations. The outer nose contains a paired cavity (vestibule) continuous with that of the olfactory chambers, and may be provided with a complicated musculature, which in diving Mammals forms a sphincter in connection with a special valvular apparatus for closing the nostrils. An excessive development and increase in the musculature, as well as an upward and backward shifting of the nasal apertures in their relation to the skull, is seen in those forms in which the external nose grows out to form a longer or shorter trunk or proboscis, at the distal end of which the nostrils open (*e.g.* Shrew, Mole, Pig,[1] Tapir, Elephant). By means of its abundant nerve-supply, the proboscis serves as a delicate organ of touch and may even give rise to a prehensile apparatus (Elephant). In the Ape *Nasalis* the peculiar and grotesque external nose, with downwardly directed nostrils, cannot be directly compared with the human external nose.

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[1] The maxillary sinus is the most constant, and is typical for the Eutheria: it usually extends into a number of neighbouring bones. In general, the pneumaticity of the skull is in direct proportion to the size of the animal: in Insectivores and Bats the maxillary sinus is the only one present.

VOMERO-NASAL (JACOBSON'S) ORGAN.

By the term "Jacobson's organ" is understood a paired accessory nasal cavity which in an early embryonic stage becomes differentiated from the nasal chamber, and which is supplied by the olfactory and trigeminal nerves.

This cavity is first met with in Amphibians, but is wanting in Proteus and Necturus. In the larvæ of Anura and Myctodera a small gutter-like medio-ventral outgrowth of each nasal cavity is formed, and in most Urodeles this later undergoes a relative change of position, so as to be situated laterally (Fig. 200, A–D): at its blind end a gland is developed. The accessory nasal chamber of Cæcilians[2] (p. 264) is developed in a similar manner (E), and a large gland is in connection with it.

The vomero-nasal organ of the Amniota is also developed in the medio-ventral part of the nasal chamber, close to the septum nasi. It loses its primary connection with the former, but in Hatteria, Lacertilia, and Ophidia retains its median position, lying between the floor of the nasal cavity and the roof of the mouth. It is lined by an olfactory epithelium and communicates in front with the mouth through the nasopalatine canal. A papilla usually extends into its cavity from the floor (Figs. 194 and 260, F). These organs are not present in Crocodiles, Chelonians, and Birds, but more or less distinct indications of them have been described in the embryo in some cases.

Amongst Mammals, Jacobson's organ is well marked in Monotremes (Fig. 200, G), in which it is much more highly developed than in most Lizards (except Monitors).[3] It contains a well-marked,

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[1] The external nose may be further supported by a median pre-nasal bone (*e.g.*, Mole, Pig). In Chrysochloris it is capped by a horny shield, and in Condylura its flat disc is provided with numerous tactile appendages.

[2] A curious apparatus exists in the Gymnophiona in connection with the nasal cavity and orbit. It consists of a retractile tentacle, a fibrous capsule with muscles, and a large gland, opening near the snout. Its function is not thoroughly understood, and the same is true of the tentacle-like "balancers" of larval Urodela and Aglossa.

[3] In the Australian Bat, *Miniopterus*, it is even larger relatively than in Monotremes.

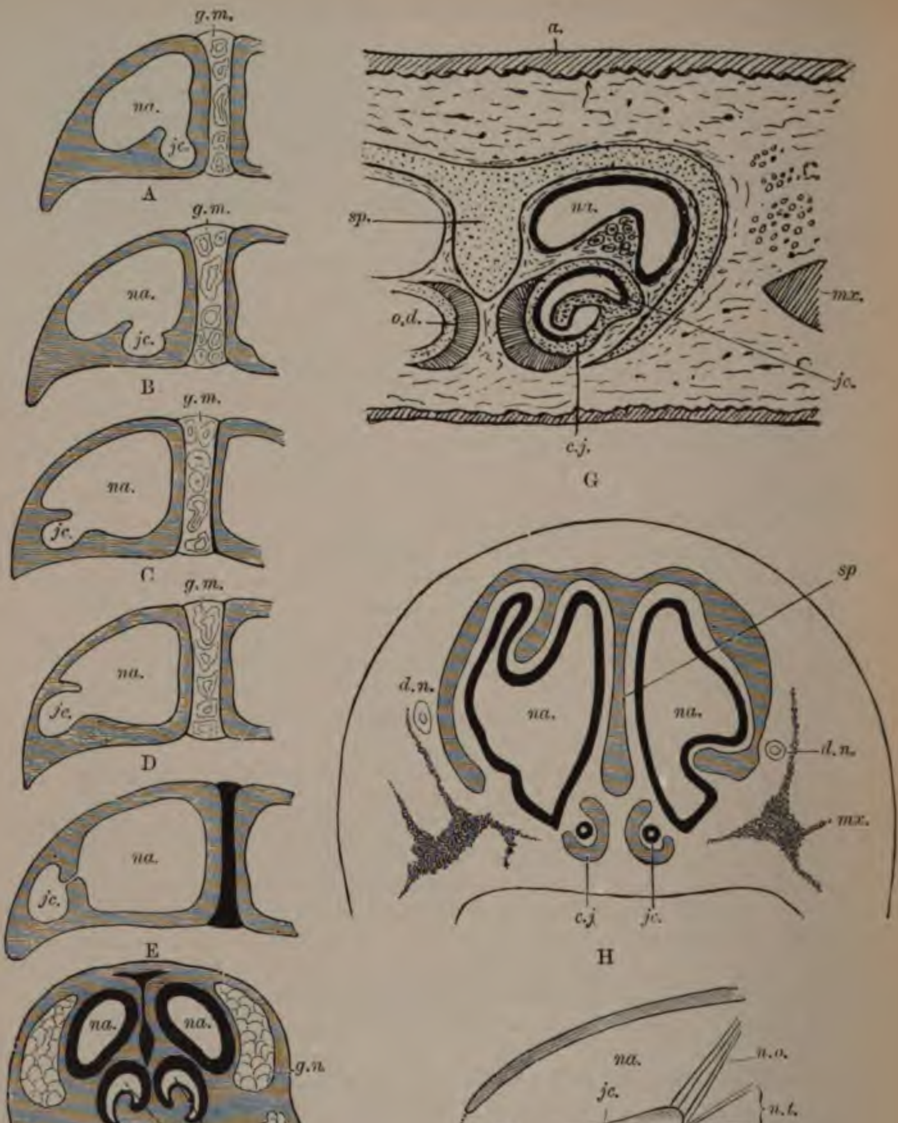


FIG. 200.—SECTIONS OF THE NOSE OF VARIOUS VERTEBRATES.

A–D, Illustrating the various ontogenetic and phylogenetic stages of the Jacobson's organ of Urodeles; in A its position is median, and in D lateral. E, Gymnophiona, in which the organ becomes separated from the main nasal cavity. F, Lacerta agilis. G, Ornithorhynchus (After Symington.) H, Placental Mammal; I, the same, in longitudinal vertical section.

a, epiderm; *c.j*, Jacobson's cartilage; *d.n*, naso-lacrymal duct; *g.m*, intermaxillary gland; *g.n*, nasal gland; *jc*, Jacobson's organ; *mx*, maxilla; *na*, main nasal cavity; *n.o*, olfactory nerve; *n.t*, trigeminal nerve; *o.d*, dumb-bell shaped bone (prevomer); *sp*, septum nasi.

turbinal-like ridge, supported by cartilage continuous with that enveloping the organ and covered with ciliated epithelium, and numerous glands are present in the mucous membrane. In other Mammals (H, I) it becomes more or less reduced, though often well-marked, even in the adult, consisting of two tubes lying at the base of the septum nasi, usually enclosed by separate *paraseptal* cartilages, which, as in Lizards and Monotremes, are differentiations of the nasal septum (*e.g.* Marsupials, Edentates, Insectivores, Rodents, Carnivores, Ungulates). A branch of the olfactory nerve enters the tube posteriorly, and anteriorly the cavity of the organ communicates with the mouth through the incisive or naso-palatine canals. Vestiges of the organ exist even in Man (Fig. 199).

The function of Jacobson's organ may be concerned with bringing the food taken into the mouth under the direct control of the olfactory nerve.

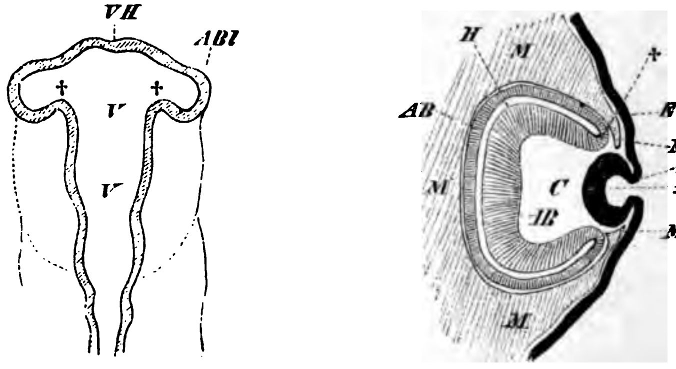
EYE.

As already mentioned, the first rudiment of the eye arises as a paired outgrowth from the primary fore-brain, known as the *primary optic vesicle* (Fig. 201, A). It, therefore, like the olfactory lobe, represents a part of the brain, and in this respect differs from the Invertebrate eye, which arises by a differentiation of the cells of the superficial ectoderm.

At the point where the vesicle touches the ectoderm, the latter becomes thickened, and the outer wall of the vesicle is asymmetrically invaginated to form a double-walled cup, the *secondary optic vesicle* (Fig. 201, B), at first open below at the slit-like *choroid fissure*. The inner and outer walls of the cup then become fused, the former giving rise in its deeper part to the sensory epithelium of the *retina*, and the latter to the *pigment epithelium*, and also to the muscles of the iris, which are thus of ectodermal origin (p. 275). As the optic vesicle grows outwards towards the outer skin of the embryo, the portion which connects it with the brain becomes constricted and by degrees loses its cavity, giving rise to a solid cord, the *optic stalk*. The fibres of the optic nerve are first differentiated in the retinal portion, and grow centripetally along the optic stalk towards the brain ; centrifugal fibres also arise later.

In the adult brain, the optic nerve is seen to arise from the diencephalon, its fibres extending upwards and backwards to the optic lobes, and three more or less sharply-differentiated portions of it may in most cases be distinguished ; these are spoken of, from the proximal to the distal end respectively, as the *optic tract*, *chiasma*, and *nerve*.

A chiasma, that is, a crossing of the fibres of the two optic nerves, doubtless always occurs though not always freely exposed, for it may retain a primitive position deeply embedded in the base of the brain (*e.g.* Myxinoids, Dipnoans, and to a certain extent in Petromyzon). In most Teleosts the optic nerves simply overlie one another (Fig. 202, A), but in some of these Fishes (Clupea (B), Engraulis), one nerve passes through a slit in the other, and this condition of things is gradually carried still further in Reptiles, until finally the fibres of the two nerves intercross in a very complicated manner (C, D), giving rise to a sort of basket-work; this is finest and most delicate in Mammals, where its structure can only be analysed by comparing a series of sections.



A B

FIG. 201, A.—DIAGRAM SHOWING THE MODE OF FORMATION OF THE PRIMARY OPTIC VESICLES (*ABl*).

VH, fore-brain; *V*, *V*, ventricular cavity of the brain, which communicates with the cavities of the primary optic vesicles at ††.

B.—SEMIDIAGRAMMATIC FIGURE OF THE SECONDARY OPTIC VESICLE, AND OF THE LENS BECOMING SEPARATED OFF FROM THE ECTODERM.

C, vitreous chamber of the eye, between the lens and retina, which later becomes filled by the vitreous humour; *H*, remains of the cavity of the primary optic vesicle; *IB*, inner layer of the secondary optic vesicle, from which the retina arises; †, point at which the latter is continuous with the outer layer (*AB*), from which the pigment epithelium is formed; *L*, lens, which arises as a cup-shaped involution of the ectoderm (*E*); *, point of involution of ectoderm to form the lens; *MM*, mesodermic tissue, which at *M*¹, *M*¹, grows in between the outer ectoderm and the lens as the latter becomes separated off, and which gives rise to the cornea as well as to the iris

To return to the further development of the eye, the ectodermic thickening mentioned above becomes separated from the ectoderm, sinks more and more into the interior of the optic vesicle, and is differentiated to form the *crystalline lens* (Fig. 201, B). It is usually at first a hollow invagination, reminding one of a primitive sensory organ of the Anamnia or of the primitive olfactory pit. On the closure of the aperture of invagination, it forms a vesicle, the thinner outer wall of which gives rise to the so-called lens-epithelium, while the cells of the thicker outer wall elongate to form the transparent fibres of which the greater part of the lens is composed.

The remaining space within the optic vesicle becomes filled by tissue[1] which extends through the so-called choroid fissure (p. 273), and gives rise to the *vitreous body* or *humour* (Fig. 201, B). Blood-vessels also extend into the vesicle in the same manner, and others arise at its periphery, where a definite vascular and pigmented membrane, the *choroid*, is formed from the surrounding mesoderm.

Internally to the lens, the choroid gives rise to the *ciliary folds*, while more externally it passes in front of the lens to form the *iris*, which retains in the centre a circular or slit-like aperture, the *pupil*, through which the rays of light pass (Fig. 203). The amount of light admitted is regulated by the dilator and constrictor (sphincter) muscles of the iris, which are able to increase or lessen the size of the pupil; the iris thus serves as a screen to regulate the amount of light which enters the eye.

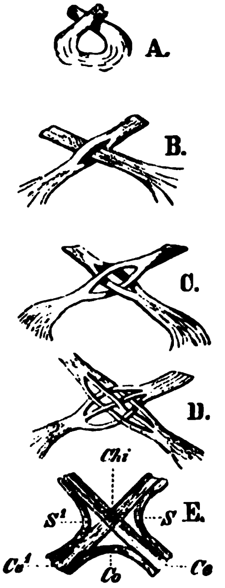


Fig. 202.—Chiasma of the Optic Nerves. Semidiagrammatic. A, most Teleostei; B, Herring; C, Lacerta agilis; D, Agama; E, Mammal.

Chi, chiasma of the bundle of nerves lying centrally (*Ce*, *Ce*¹); *S*, *S*¹, lateral fibres, which do not cross.

Not only are the size and form of the pupil inconstant, but the lens is also capable of undergoing considerable change in relative position (*e.g.* Fishes, Amphibians, Snakes) or in form, becoming more flattened or more convex, as the case may be (*e.g.* Mammals, Birds, Lizards, Chelonians): the former condition occurs when distant, the latter when near objects are looked at. This delicate accommodating apparatus in higher forms is regulated by a *ciliary muscle* (*tensor choroideæ*) supplied by the oculomotor nerve, which arises in a circle all round the eye from the point of junction of the iris and sclerotic and is inserted along the peripheral border of the iris.

Externally to the vascular layer of the choroid is a lymph-sinus with pigmented walls (*lamina fusca*), and externally to this, again, is a firm, fibrous, partly cartilaginous, or even ossified layer, the *sclerotic*, which is also surrounded by a lymph-space. The latter passes internally into the sheath of the optic nerve, which is continuous with the dura mater, and externally into the *cornea*, the outer surface of which is covered over by an epithelial layer continuous with the epiderm — the *conjunctiva*. The sclerotic and cornea together form a firm outer support for the eye, and thus, together with the gelatinous mass of the vitreous humour, guarantee the rigidity necessary for the physiological activity of the nerve end-apparatus. Between the cornea and iris there is a large lymph-space, the *aqueous chamber*, its contained fluid being called the *aqueous humour*: extending around the chamber is a venous plexus, which is bathed by the aqueous humour.

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[1] By some embryologists this tissue is said to be ectodermic, and not mesodermic in origin, except as regards the evanescent embryonic blood-vessels.

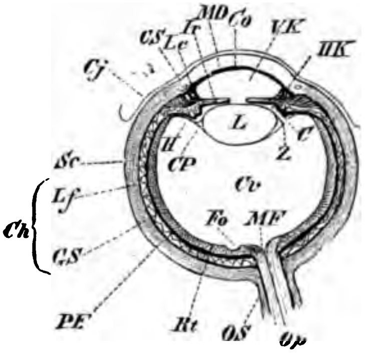

FIG. 203.—DIAGRAM OF A HORIZONTAL SECTION THROUGH THE LEFT HUMAN EYE, seen from above.

C, ciliary process; *Ch*, choroid, with its lamina fusca (*Lf*) and vascular layer (*GS*); *Cj*, conjunctiva; *Co*, cornea; *CP*, canal of Petit; *CS*, venous plexus (canal of Schlemm); *Cr*, vitreous chamber; *Fo*, yellow spot (fovea centralis); *H*, hyaloid membrane; *HK*, so-called posterior chamber; *Ir*, iris; *L*, lens; *Lc*, ciliary ligament; *MD*, posterior elastic lamina (membrane of Descemet); *MF*, blind-spot; *Op*, optic nerve; *OS*, sheath of optic nerve; *Rt*, retina; *PE*, pigment epithelium of retina; *Sc*, sclerotic; *VK*, aqueous chamber; *Z*, Zonula ciliaris (zone of Zinn).

The relative development of the eye is affected by the external conditions,[1] and is in general proportional to the rapidity of the movements performed by the animal concerned and to the relative development of the mid-brain.

In all Vertebrates the eyeball is surrounded by a membranous, sac-like investment (the *periorbita*), which arises in the region of the optic foramen and radiates outwards towards the skin, its distinctness being less marked the more completely the orbit is surrounded by skeletal parts. As in most Vertebrates the cavity of the orbit is more or less continuous with the temporal and oral cavities, the orbital sac has a close relation to the muscles of the jaws, certain portions of which may invade it and take on functional relations to the optic apparatus (Amphibia, Sauropsida). Only in the higher Mammals (*e.g.* Primates) is the orbit almost completely surrounded by bone and thus separated from the masticatory muscles, and in this case the periorbita is more or less closely applied to or fused with the orbital periosteum.

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[1] The adaptive modifications of the eye are very varied amongst Vertebrates. It may reach a very high degree of perfection; or may, on the other hand, undergo more or less degeneration in those animals which live in caves or burrows, or in the deep sea (*e.g.* *Fishes*—Amblyopsis spelæus, Troglichthys, Typhlogobius; *Amphibians*—Proteus, Spelerpes maculicauda, Typhlotriton, Typhlomolge, Gymnophiona; *Reptiles*—Typhlops vermicularis, Rhineura floridana; *Mammals*—Notoryctes typhlops, Talpa). In the Cetacean Platanista gangetica the eyes are extremely minute. The reduction of the eyes in many deep-sea Fishes may be compensated for by the special development of tactile organs. (Cf. also under Cyclostomes, p. 278).

The deep orbit, formed by the skull, serves as a further protection for the eye, in connection with which there are also certain accessory structures, viz.:—

1. *Eyelids* (*palpebræ*).
2. *Glandular organs.*
3. *Muscles* for moving the eye-ball.

Thus the eye-ball is formed of a series of concentric layers, which are called from within outwards—*retina* (sensitive and nervous layer), *choroid* and *iris* (vascular layer), and *sclerotic* and *cornea* (skeletal layer). The first corresponds with the nervous substance of the brain, the second with the pia mater, and the third with the dura mater. The interior of the eye contains refractive media, viz., the *lens* and *vitreous humour.* In addition there are the above-mentioned *accessory structures*: these, as well as the retina, will be dealt with after a description of the eyes of the various Classes of Vertebrates has been given.

Before concluding this introductory section, it must be again pointed out that the mode of development of the vertebrate eye differs markedly from that of other sensory organs in not being derived directly from the outer ectoderm, and in that the optic nerve is not an ordinary peripheral nerve, but a conducting tract passing between different parts of the central organ itself—that is, between the retina and brain. On the other hand, it must be borne in mind that the sensitive elements are developed in that part of the retinal layer which is originally continuous with the outer border of the ectoderm—that is, from the same layer as that which gives rise to the other sensory organs and the central nervous system.

Amphioxus.—Paired eyes, comparable to those of the Craniata, are wanting in the Acrania.

In addition to an unpaired pigment-spot in the front wall of the cerebral vesicle, which is supposed to serve as a light-perceiving organ, a series of simple cup-like structures, somewhat resembling the eyes of Flat Worms, are situated on either side of the spinal cord (Fig. 204). These structures are arranged in groups, corresponding to the myomeres, and gradually becoming less numerous in passing backwards to the tail. Each of these bodies is described as consisting of a single optic cell with a nerve fibre, and is partly surrounded by a pigment cell. More dorsally, above the oral region, somewhat similar, but pigmentless, bodies have been observed.

Cyclostomes.—The eye of Cyclostomes is at a very low stage of development, and has evidently undergone partial degeneration: this is indicated, not only by the structure of the retina, but also, in Myxinoids, in which the choroid fissure persists, by the absence of the lens, iris, and of a differentiated sclerotic and cornea as well as of eye-muscles. Moreover, the eye in Myxinoids and in the larval Petromyzon lies beneath the skin and subdermal connective tissue, but in the latter the skin covering the eyes becomes thinned out, and thus the animal, which was blind, or nearly blind, in the larval state, can see after undergoing metamorphosis: at the same time the eye becomes more highly organised, though the primary lumen in the lens (cf. p. 274) does not entirely disappear.

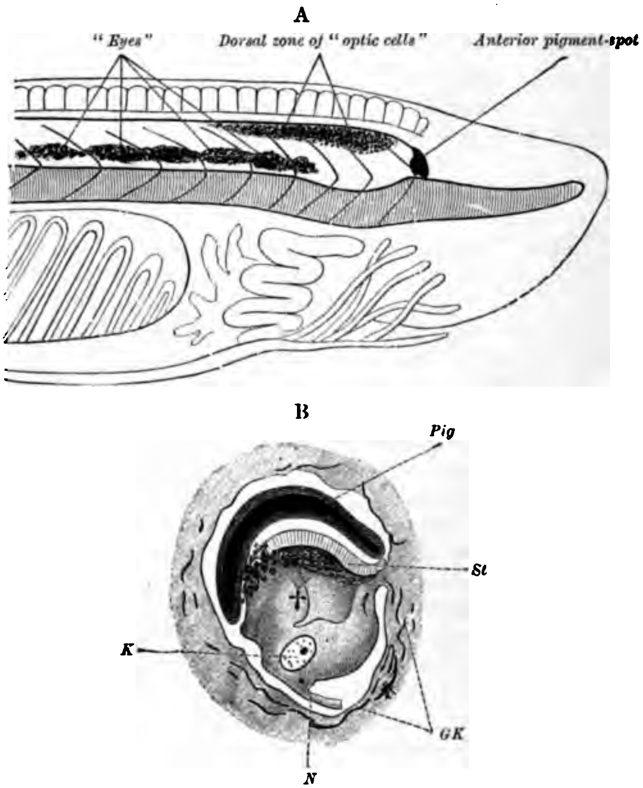

FIG. 204.—A.—THE ANTERIOR PORTION OF *Amphioxus lanceolatus*. (Modified from H. Joseph.)

B.—ONE OF THE EYE-LIKE ORGANS IN A. (After H. Joseph.)

GK, capsule, with neuroglia elements; *K*, nucleus of optic cell; *N*, its nerve-process, and †, its granular border; *Pig*, pigment-cell, showing three layers; *St*, striated border of optic cell.

Fishes.—The eyes of all the true Fishes are, with few exceptions, of considerable size, and are formed on essentially the same plan as that described in the introductory portion of this chapter.

The eye-ball is almost always surrounded by a gelatinous substance, penetrated by connective tissue fibres, and in many Elasmobranchs it is articulated on its inner circumference with a rod of cartilage connected distally with the lateral wall of the skull. The sclerotic is usually extensively chondrified, and not infrequently becomes calcified or ossified towards its junction with the cornea.

The lens of Fishes is globular, or nearly so, and possesses therefore a high refractive index. It touches the cornea and fills up the greater part of the eye-ball, so that only a small space is left for the vitreous humour. It differs from that of other Vertebrates in the fact that, in the condition of rest, it is accommodated for seeing near objects. Fishes possess no ciliary muscle, and in many of them (most Teleostomi) accommodation takes place by means of a process of the choroid, the *processus falciformis*. This extends through the embryonic choroid fissure into the vitreous humour towards the lens, around which it expands to form the so-called *campanula Halleri*, which is often pigmented (Fig. 205). In the interior of this structure are nerves, vessels, and smooth muscle-fibres, and the latter exert an influence on the lens, drawing it towards the retina. The processus falciformis is small in Ganoids and certain Teleosts, is apparently absent in Cyclostomes and Dipnoans, and is probably represented in Elasmobranchs, at any rate in the embryo: how accommodation is effected in these Fishes is not known.

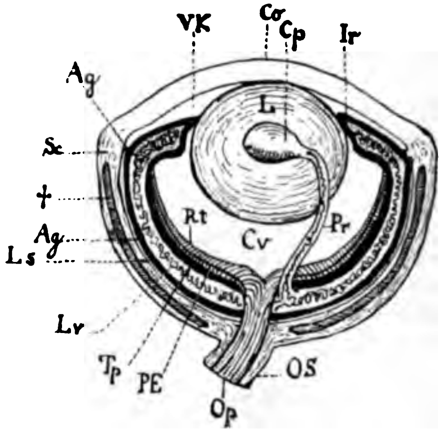

FIG. 205.—DIAGRAM OF THE EYE IN A TYPICAL TELEOST.

Ag, argentea; *Co*, cornea; *Cp*, campanula Halleri; *Cr*, vitreous body; *Ir*, iris; *L*, lens; *Ls*, lamina suprachoroidea; *Lv*, lamina vasculosa; *Op*, optic nerve; *OS*, sheath of optic nerve; *PE*, pigment epithelium; *Pr*, processus falciformis; *Rt*, retina; *Sc*, sclerotic, with cartilaginous and osseous (†) portions; *Tp*, tapetum; *VK*, aqueous chamber.

The iris of Fishes takes no part in accommodation, and only appreciably reacts to light or electric stimuli in a few species living in shallow water in which the eyes are directed upwards.

Externally to the choroid proper, and internally to the suprachoroideal lymph-space, is a silvery or greenish-gold iridescent membrane, the *argentea*. It extends either over the whole interior of the eye (Teleosts), or is limited to the iris (Elasmobranchs). A second layer with a metallic lustre, the *tapetum lucidum*, is present in Elasmobranchs internally to the iridescent portion, and within this again is the layer of the choroid known as the choriocapillaris. No tapetum appears to be present in Teleostei or Petromyzon.

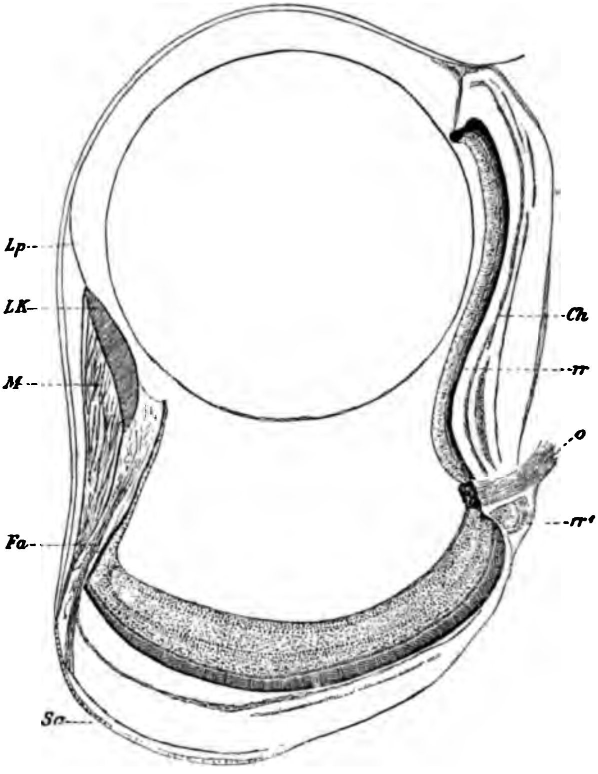

FIG. 206.—LONGITUDINAL VERTICAL SECTION OF THE EYE OF DISSOMMA. (After A. Braner.)

Ch, choroid; *Fa*, fibres of the argentea; *LK*, lens-cushion; *Lp*, ligamentum pectinatum; *M*, smooth muscle; *o*, optic nerve; *rr*, accessory retina; *rr'*, portion of accessory retina; *Sc*, sclerotic.

The so-called "*choroid gland*," present in many Teleostei and in Amia, consists of a network of blood-vessels (rete mirabile) which has the form of a cushion, lying near the entrance of the optic nerve, between the argentea and pigment epithelium of the retina; it thus has nothing to do with a "gland," and is in relation to the pseudobranch (cf. under Respiratory and Vascular organs).

The eyes of certain deep-sea Teleosts are of particular interest, as they are adapted in a remarkable manner both as regards position and structure to the special conditions under which these Fishes live in comparative darkness. In most Fishes, the laterally situated eyes are capable of monocular vision only, while most deep-sea forms possess binocular " telescopic " eyes, the axis of the two organs being nearly parallel. The eye-ball, moreover, is much elongated (Fig 206), so that there is a considerable distance between its inner wall and the lens; the latter is especially large, and the cornea is very convex and forms a considerable part of the wall of the eye-ball; the iris is almost entirely wanting; and finally, the retina is differentiated into a main portion and a small accessory portion—usually situated only on that part of the wall which is nearest to the median line of the head. The eye-muscles are more or less reduced and shifted in position, while the apparatus for accommodation, the suspensory ligament and retractor of the lens, are well developed. These modifications result in allowing as many rays of light as possible to enter the eye and spread out over the retina.[1]

In the Flat-fishes (Pleuronectidæ), which have acquired the habit of swimming and lying on the bottom on one side, the eye of the lower side gradually rotates so as to reach the upper surface.

In Dipnoans the eye is relatively small as compared with that of other Fishes. In Protopterus the sclerotic is partly cartilaginous, and the lens is globular and relatively large. As already mentioned, there is apparently no processus falciformis, and a tapetum, argentea, and " choroid gland " are wanting. On the whole, the eye is intermediate in structure between that of Ganoids and that of Urodeles.

Amphibians.—The eyes of Amphibians are in general relatively small, and do not exhibit any essential advance in structure as compared with those of Fishes: in certain respects they show negative characters as compared with the latter, for an argentea, a tapetum, a "choroid gland," and a processus falciformis and campanula Halleri are wanting.

The eye-ball is nearly globular and the cornea moderately convex; the pupil is round, or occasionally three-cornered (Bombinator). The large lens is more convex on its inner than on its outer surface, especially in Anurans, and the larvæ usually have a smaller lens-index than adults. Accommodation does not take place by an alteration in form of the lens, but in some cases, apparently, the lens can be shifted towards the cornea by the action of the ciliary muscle.[2] Ciliary processes can be recognised in Urodeles, but are much more distinct in Anurans, and the iris has well-developed smooth muscles. The sclerotic, as in Fishes, encloses hyaline cartilage and is often pigmented: ossifications are not known to occur.

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[1] In Periophthalmus and Boleophthalmus the structure of the eye is peculiarly modified for vision in the air as well as in the water.

[2] A protractor of the lens, consisting of smooth fibres, occurs amongst Urodeles and in the Frog, the fibres, however, taking a different course in the two cases. It is not known whether this muscle is the homologue of the retractor of the lens in Fishes.

Reptiles and Birds.—In the Sauropsida, more especially in Birds, the eye-ball is much larger relatively to the head than in the Amphibia. The sclerotic here, too, is in great part cartilaginous, and in Lizards and Chelonians is provided with a ring of delicate bony *sclerotic plates* around the external portion. Many fossil Reptiles and Amphibians possessed similar plates, as do also existing Birds (Figs. 207, 208); in Birds horseshoe-shaped or ring-shaped bony structures are also usually present close to the entrance of the optic nerve.

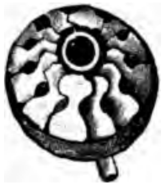

FIG. 207. — EYE OF *Lacerta muralis*, SHOWING THE RING OF BONY SCLEROTIC PLATES.

The eyeball of Reptiles has a more or less globular form, while that of Birds, more especially nocturnal Birds of prey (Owls), is more elongated and tubular, an external larger segment being sharply marked off from an internal smaller one, the outer portion being bounded externally by the very convex cornea and enclosing a large aqueous chamber: moreover, the whole eye is relatively larger (Fig. 208). In all the Sauropsida, except Snakes, there is a complicated ciliary muscle composed of striped fibres, one portion of which, extending towards the cornea, is known in Crampton's muscle; ciliary processes are well developed, especially in Birds. This muscle is also transversely striated in Reptiles, and, especially in Chelonians, is always well developed, though not to such an extreme degree as in Birds.

In Reptiles (*e.g.* Lizards) a tapetum may be developed, but an argentea and "choroid gland" are never present; all these parts are wanting in Birds. A cone-like or cushion-like structure, the so-called "*pecten*," which is to some extent homologous with the processus falciformis of Fishes, is, however, present in Lizards, but is more or less reduced in other Reptiles. It varies much in its development in different forms, is very vascular and sometimes pigmented, and extends into the vitreous chamber through the proximal end of the choroid fissure. In Birds,[1] a somewhat similar organ is very largely developed, and in some cases may even extend as far as the capsule of the lens: it is four-cornered, more or less folded, and pigmented, and consists mainly of a closely-felted network of capillaries. From its form, it is better described in Reptiles as a "*cone*" or "*cushion*" and in Birds as a "*fan*" (Fig. 208). In both Reptiles and Birds this organ appears, amongst other possible functions, to be important in connection with the nutrition of the contents of the eyeball and of the retina: it has nothing to do with accommodation.

The iris, regulated by striated muscle, is able to respond very quickly to visual impressions: it is often brightly coloured, owing to the presence, not only of pigment, but also of coloured fat globules. The pupil is as a rule round, but in many Reptiles and in Owls has the form of a vertical slit. The form, structure, and relative size of the lens varies considerably: amongst Reptiles, its refractive index is lowest in Snakes, and highest in Lizards (except Geckos). In many Birds it has a very peculiar form. The mechanism of accommodation in some Snakes resembles that seen in Amphibians (p. 281), while in the other Sauropsida the ciliary muscle, acting on the capsule of the lens, is able to alter the curvature of the latter, as is also the case in Mammals.

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[1] In Apteryx the pecten disappears during development.

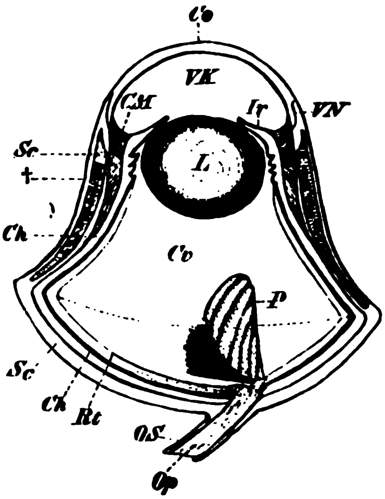

FIG. 208.—EYE OF AN OWL.

Ch, choroid; *CM*, ciliary muscle; *Co*, cornea; *Cv*, vitreous chamber; *Ir*, iris; *L*, lens; *Op*, *OS*, optic nerve and sheath; *P*, "fan" (pecten); *Rt*, retina; *Sc*, sclerotic, with its bony ring at †; *VK*, aqueous chamber; *VN*, point of junction between sclerotic and cornea. The dotted line around the broadest portion of the circumference, divides the eye into an inner and an outer segment.

Mammals.—In Mammals the eyeball, especially in Primates, is more completely enclosed within the bony orbit than is the case in most other Vertebrates, and this may partially account for the fact that, except in Monotremes, the sclerotic no longer shows traces of cartilage or bone, but is entirely of a fibrous character: in Whales it is extremely tough. Excepting in aquatic Mammals, in which it is somewhat flattened, the cornea is moderately convex, and the whole eyeball is of a more or less rounded form.

A *tapetum lucidum*, consisting either of cells or fibres, exists in the choroid of numerous Mammals, and gives rise by interference to a glistening appearance when seen in the dark (Carnivora, Ruminants, Perissodactyla, &c.). In some Mammals there is a differentiation of the capillary vessels (membrana choriocapillaris) from the larger arterial trunks of the choroid: the veins are situated externally to the arteries. Certain structures homologous with the processus falciformis or pecten are present in Mammals in the embryo only.

The ciliary muscle consists of smooth elements. The external surface of the lens is less convex than the internal, which latter lies in the so-called fossa patellaris of the vitreous humour. The pupil is not always round, but may be transversely oval (*e.g.* Ungulates, Kangaroos, Cetaceans), or slit-like and vertical (*e.g.* Cat).

Retina.

The fibres of the optic nerve, which pass into the eyeball at a right or acute angle, cross one another at the point of entrance, and are then distributed to the sensitive elements of the retina. The latter is thus thickest at the point of entrance of the nerve, which is known as the "blind spot" (Fig. 203), and gradually decreases in thickness towards the ciliary processes until, at the point of origin of the iris, it consists of a single layer of cells.

The retina is bounded on its outer periphery by a structureless hyaline membrane (*limitans externa*),[1] while on its inner side it is covered by the *hyaloid membrane*, which, strictly speaking, belongs to the vitreous humour. The retina is quite transparent in the fresh condition, and consists of two portions which are histologically and physiologically quite distinct: they are, a *supporting part* and a *nervous part.* The former is stretched as on a frame between the limitans externa and hyaloid membrane.

The nervous elements are arranged in the following concentric layers:—

I. *Developed from the internal layer of the secondary optic vesicle,*
A. *Cerebral layer.*
  1. Layer of nerve-fibres (of optic nerve).
  2. Layer of ganglion-cells.
  3. Inner reticular layer.
  4. Granular layer (inner).
  5. Outer reticular or subepithelial layer.
B. *Epithelial layer.*
  6. Layer of visual cells (outer granular layer with the rods and cones).

II. *Developed from the external layer of the secondary optic vesicle.*
  7. Pigment epithelium (retinal epithelium).

These layers are so arranged that the nerve-fibres lie next to the vitreous humour, that is, internally, while the rods and cones are situated towards the choroid, *i.e.* are external. Thus the terminal members of the neuro-epithelium are turned away from the rays of light falling upon the retina, and the rays must therefore pass through all the other layers before they reach the rods and cones.[2]

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[1] The limitans externa encloses the entire retina externally in the embryo, but later the rods and cones come to project through it (cf. Fig. 209).

[2] Fishes possess the longest, Amphibians the thickest rods, so that in the latter there are only about 30,000 to a square millimetre, while in Man there are from 250,000 to 1,000,000. In Fishes, Birds, and Mammals the rods (which are the phyletically older structures) far exceed the cones in number, while in Reptiles the reverse is the case: in Petromyzon and Elasmobranchs, for example, *there are no cones* at all. In some Reptiles there are no rods, and in nocturnal

In the retina of all Vertebrates there is a specially modified region of most acute vision. This is called the *yellow-spot* (*fovea centralis* or *macula lutea*), and is due to the thinning-out of all the layers except that of the neuro-epithelium, and even the rods disappear, only the cones persisting (Fig. 203). A yellow spot is wanting in most Fishes, in Urodeles, and in certain Mammals (*e.g.* Insectivores, Rodents), and is only slightly marked in the Anura and most Sauropsida, but in Birds there may be two "yellow spots." Only in Mammals does the retina possess special blood-vessels, and even in certain of these they may be reduced or wanting. In other Vertebrates (except the Eel) the retina is non-vascular, and is nourished by the vessels of the vitreous body, processus falciformis, or "pecten."

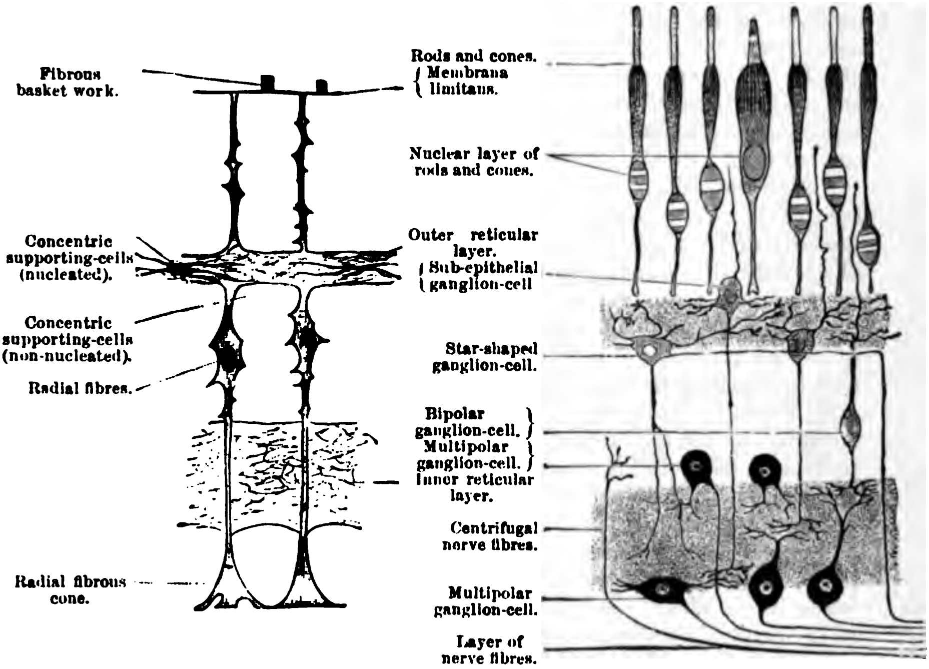
Fibrous basket work.
Concentric supporting-cells (nucleated).
Concentric supporting-cells (non-nucleated).
Radial fibres.
Radial fibrous cone.
Rods and cones.
Membrana limitans.
Nuclear layer of rods and cones.
Outer reticular layer.
Sub-epithelial ganglion-cell
Star-shaped ganglion-cell.
Bipolar ganglion-cell.
Multipolar ganglion-cell.
Inner reticular layer.
Centrifugal nerve fibres.
Multipolar ganglion-cell.
Layer of nerve fibres.

Fig. 209.—Diagram of the Elements of the Retina. (Supporting elements on the left, and nervous elements on the right.) (After Ph. Stöhr.)

animals the rods are more numerous than the cones. The cones of many Reptiles, of Birds, and of Marsupials, are distinguished by the presence of brightly coloured oil-globules.

Accessory Organs in Connection with the Eye.

(*a*) EYE-MUSCLES.

The movement of the eye-ball is in general (except in Myxinoids, cf. p. 278) effected by six muscles, four of which are known as the *recti* (superior, inferior, external or posterior, and internal or anterior), and two as the *obliqui* (superior and inferior). The former, which arise from the inner portion of the orbit, usually from the dural sheath of the optic nerve, together circumscribe a pyramidal cavity, the apex of which lies against the inner portion of the orbit, while the base surrounds the equator of the eye-ball, where the muscles are inserted into the sclerotic.

Both the oblique muscles usually arise from the anterior or nasal side of the orbit, and as they respectively pass from this region dorsally and ventrally in an equatorial direction round the eye-ball, they constitute a sort of incomplete muscular ring.[1]

Besides these six muscles, others are usually present from the Amphibia onwards. Of these, the *retractor bulbi*, which often consists of several portions, is derived genetically from the posterior rectus, and is supplied by the abducent nerve. In Amphibians, Reptiles, and Birds, a portion of the striated masticatory musculature, supplied by the trigeminal, extends into the fibrous walls of the periorbita (p. 276), and in Rana, for example, gives rise to an elevator of the eye-ball, a depressor of the lower eyelid, and a kind of extensor of the lower wall of the orbital sac, the connection of which with the masticatory muscles is plainly seen. In Anurans there is also a more ventral, transverse layer, corresponding to the depressor of the lower lid in Lizards and Birds, in which latter there is also a layer in the orbital membrane corresponding to the depressor of the lower orbital wall in Amphibians.

As the transversely striped periorbital muscles gradually become of less importance in the Vertebrate series, the smooth muscles are further developed. The latter are already indicated in Teleosts; but in Reptiles (especially Lizards and Chelonians) are much more marked, and are continued into the eyelids. In Mammals, the development of the smooth orbital musculature varies considerably, and is less marked the more the orbit is enclosed by bone (*e.g.* in Primates, in which it lies in the infra-orbital fissure). It, like the upper and lower palpebral muscles, which are specially important in Mammals, are supplied by the sympathetic.

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[1] A deviation from this arrangement is seen in Mammals, in which the superior oblique has gradually come to arise from the inner part of the orbit, and then passes forwards towards its anterior (internal) angle, where it becomes tendinous, and passes through a fibro-cartilaginous pulley (trochlea) attached to the upper border of the orbit, on the frontal bone. Hence it is sometimes called the trochlear muscle. From this point it changes its direction, and becomes *reflected* obliquely outwards and backwards to the globe of the eye.

(*b*) EYELIDS (PALPEBRÆ).

In Fishes and other lower aquatic forms the upper and lower eyelids are usually very rudimentary, having at most the form of stiff folds of the skin, and in all other Vertebrates below the Mammalia they never reach a very high stage of development: even in those Mammals in which the facial muscles are not much differentiated they are not greatly specialised. They are lined on the inner surface by a continuation of the epiderm, the *conjunctiva*, which is continued over the cornea (Fig. 203),[1] and in the Ichthyopsida are usually not sharply marked off from the rest of the skin, and are capable at most of very slight movement: the eyelids in these forms therefore only protect the eye to a slight extent, and allow it comparatively little free movement.[2]

In the Sauropsida they are in certain respects much more highly differentiated. Occasionally (Chameleon) they are circular and are movable by muscles, while in Geckos, Amphisbænians, and Snakes the two eyelids grow together to form a transparent membrane overlying the eye, and this comes away with the rest of the outer part of the skin when it is shed.

A levator of the upper lid, which latter is usually the better differentiated of the two and which in many Reptiles and Birds may be supported by a membrane-bone or fibro-cartilage, occurs in Chelonians, Crocodiles, Birds, and Mammals. Lizards, Chelonians, Birds, and many Mammals (*e.g.* Ungulates) possess a depressor of the lower lid.

In Mammals, the eyelids, more particularly the upper one, are extremely movable, and may be provided with hairs (eyelashes) on their free margin. In their interior a hard body, the so-called "lid-cartilage," enclosing the Meibomian glands, is developed (Fig. 210, B), and they are closed by a circular muscle (*orbicularis* or *sphincter oculi*) which surrounds the whole slit between the lids, and is a derivative of the mimetic musculature.

The want or comparatively slight development of upper and lower eyelids in Vertebrates below the Mammalia is compensated for in certain forms, at any rate to a certain extent, by the presence of a *nictitating membrane*.[3] This "*third eyelid*" differs from the others in having nothing to do with the outer skin proper, consisting simply of a reduplicature of the conjunctiva, and being regulated by special muscles supplied by the abducent nerve, and known in Reptiles and Birds as the *quadratus* (*bursalis*) and *pyramidalis*, which are genetically related to the retractor bulbi.

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[1] In Fishes and Amphibian larvæ the conjunctiva retains essentially the same structure as the epiderm from which it is derived, while in higher forms it undergoes modifications, and the stratum corneum becomes less horny.

[2] Accessory lid-folds occur, *e.g.*, in the Herring and Salmonidæ.

[3] The structure known as a "nictitating membrane" in many Elasmobranchs is not exactly comparable to the nictitating membrane of higher Vertebrates. It is secondarily derived from the lower lid-fold, and is provided with several muscles, supplied by the trigeminal (or facial) nerve, and derived from integumentary muscles in the region of the spiracle.

The nictitating membrane, which may enclose a cartilage, is situated within the lower eyelid, or it may lie more towards the anterior angle of the eye. The former condition is seen, *e.g.*, in Anurans and the latter in Birds, in which a third eyelid is so largely developed as to be capable of covering the whole freely exposed portion of the eye-ball. In Mammals also it is situated in the anterior angle of the eye, and in Primates becomes reduced to a small, half-moon-shaped fold (*plica semilunaris*).

(*c*) GLANDS.

The glands in connection with the eye are: (1) the *lacrymal*, (2) the *Harderian*, or gland of the nictitating membrane, and (3) the *Meibomian glands*.

The secretions of all these serve to keep the free surface of the eye-ball moist, and to wash away foreign bodies. In Fishes the outer medium appears to suffice for this purpose, but the first attempt of a Vertebrate to exchange an aquatic for an aërial existence necessitated the development of a secretory apparatus in connection with the eye.

Thus in Urodeles a glandular organ is developed from the conjunctival epithelium along the whole length of the lower eyelid; in Anurans and Reptiles this becomes more developed in the region of the anterior, and in many Reptiles also of the posterior, angle of the eye, the original connecting bridge gradually disappearing: thus two glands are developed from the primitively single one, each of which becomes further differentiated both histologically and physiologically. From one is formed the *Harderian gland*,[1] which is situated at the anterior angle of the eye, surrounding to a great or less extent the antero-ventral portion of the eyeball, while the other gives rise to the *lacrymal gland* (Fig. 210). The latter retains throughout life its primitive position at the posterior angle of the eye, and even in Birds lies in the region of the lower eyelid, and is supplied by the second division of the trigeminal. In Mammals it becomes gradually further subdivided, and extends into the region of the upper eyelid, so that its ducts open above the eye into the upper conjunctival sac. Nevertheless, even in the Primates, in which it consists of two parts, more or fewer ducts are present which open into the lower conjuctival sac, and thus the primitive position of the lacrymal gland is indicated.

The secretion usually passes by several ducts into the conjunctival sac, where it would accumulate were it not for the fact that the movement of the lids drives it towards the anterior (inner) angle of the eye, where the *puncta lacrymalia* are situated, often on small papillæ. These lead into short ducts communicating with the so-called lacrymal sac which opens into the naso-lacrymal duct. A well-differentiated Harderian gland, sometimes consisting of histologically and physiologically different elements, is present from the tailless Amphibia to the Mammalia, but is rudimentary in the Primates.

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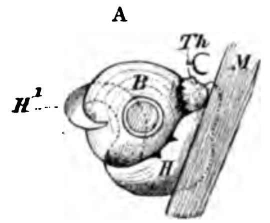
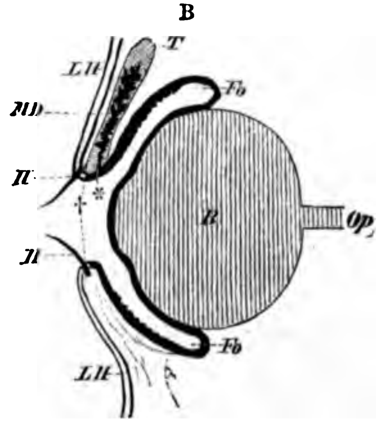
[1] In Crocodiles, Snakes, and Hatteria the lacrymal gland is wanting, while in Chelone it is extremely large.





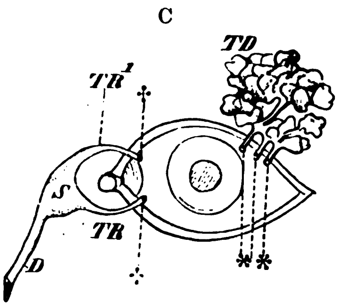


Fig. 210.—A. Harderian Gland (*H*, H^1) and Lacrymal Gland (*Th*) of *Anguis fragilis*.

B, eyeball; *M*, muscle of jaw.

Fig. 210.—B. Diagrammatic Transverse Vertical Section through the Eye of a Mammal.

B, eyeball; *Fo*, *Fo*, upper and lower conjunctival sac; *H*, *H*, eyelashes; *LH*, *LH*, outer skin of the eyelids, which at the free edges of the latter, at †, becomes continuous with the conjunctiva; *Op*, optic nerve; *T*, the so-called tarsal fibro-cartilages, in which the Meibomian glands (*MD*) lie embedded, the latter opening at *.

Fig. 210.—C. Diagram of the Lacrymal Apparatus of Man.

D, naso-lacrymal duct; *S*, lacrymal sac; *TD*, lacrymal gland, divided up into several portions; *TR*, TR^1, upper and lower lacrymal canals; **, ducts of the lacrymal gland; ††, puncta lacrymalia.

The *Meibomian glands* (Fig. 210, B) are confined to the Mammalia, and lie embedded in the substance of the eyelids in the form of branched, tree-like tubes or clustered masses. They open on the free edge of the lid, produce a fatty secretion, and originally correspond to true sebaceous glands developed in connection with hair-rudiments, the hairs disappearing but the glands remaining. They are wanting in some Mammals (*e.g.* Monotremes, Armadillo, Manis, Dolphin, Seal, Elephant, Camel). Certain modified sweat-glands known as the *glands of Moll* are also present within the eyelids of Mammals, opening on the margins of the lids close to the eyelashes.[1]

AUDITORY ORGAN.

Certain relations to the integumentary sense-organs of Fishes and Amphibians can be traced in the organs of taste (p. 254), and the same is true of the auditory organ, the function of which is concerned with equilibration as well as with hearing: in all three cases the sensory epithelium is derived directly from the ectoderm.

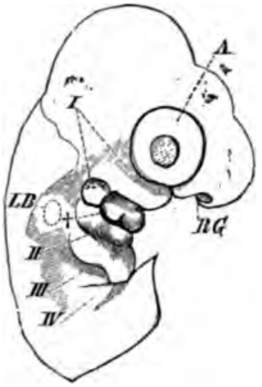


FIG. 211.—HEAD AND ANTERIOR PORTION OF BODY OF A CHICK. (In part after Moldenhauer.)

A, eye; *LB*, primitive auditory vesicle seen through the wall of the head; *RG*, olfactory pit; †, point at which the external auditory passage begins to be formed; *I* to *IV*, first to fourth visceral arches.

The first trace of the auditory organ is seen as a thickening of the ectoderm (*auditory plate*) on either side of the primary hind-brain between the trigeminal nerve and vagus group, which becomes invaginated and separated off to form a vesicle (Fig. 211), the epithelium of which eventually undergoes differentiation into elongated cells of sensory epithelium provided with hair-like processes, and supporting cells (Fig. 212), as in that of the integumentary sense-organs referred to above. The sensory cells are in relation with nerve-fibres which arise from the auditory ganglion.

After the vesicle of either side has become separated off from the ectoderm, it sinks deeper and deeper into the mesodermic tissue of the skull, loses its original pyriform or rounded shape, and becomes divided into a superior and an inferior part, called respectively the *utriculus* and *sacculus*, at first connected with one another by a wide utriculo-saccular canal (Fig. 213). From the former the so-called *semicircular canals* become developed, while from the latter the tube-like *ductus endolymphaticus* and the *lagena* (*cochlea*) are formed.

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[1] In Cetaceans the whole lacrymal apparatus has undergone degeneration in adaptation to the external conditions, and the nictitating membrane is vestigial: well-developed lacrymal and Harderian glands are present in the embryo. A greater or less reduction of the lacrymal gland may also occur in other Mammals, *e.g.* Seal, Hippopotamus, Elephant, Otter, and Mole.

The whole of this complicated apparatus constitutes the *internal ear* or *membranous labyrinth*. It becomes surrounded secondarily by mesodermic tissue, which is at first gelatinous and in close contact with it. A process of absorption then takes place in the innermost layers of the mesoderm, and thus a space is developed which closely repeats the form of the membranous labyrinth, as does also the mesoderm which encloses this space and which later becomes chondrified, and often also ossified. A *membranous* and a *cartilaginous* or *bony labyrinth* can thus be distinguished, and between them is a cavity (*cavum perilymphaticum*) filled with a lymph-like fluid (*perilymph*), and penetrated by connective tissue and blood-vessels extending from its walls to the membranous labyrinth. The cavity within the latter, which also contains a fluid (*endolymph*), is spoken of as the *cavum endolymphaticum*.

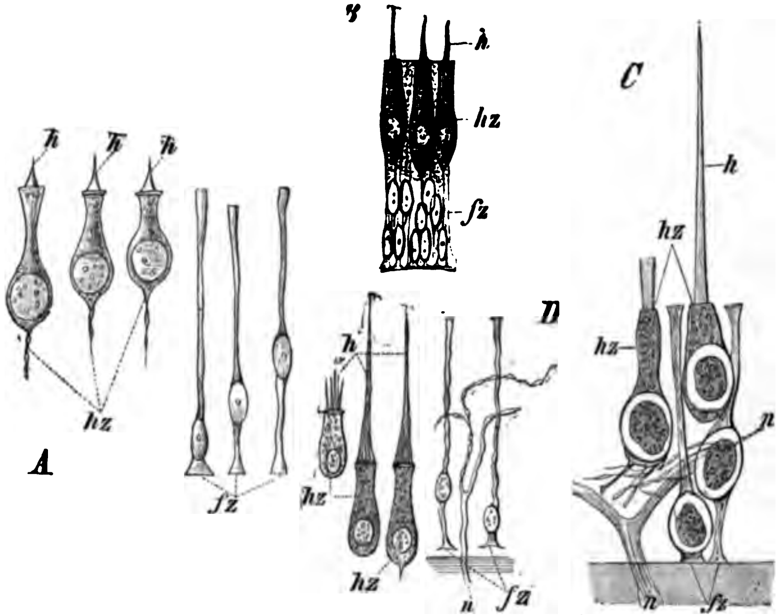

FIG. 212.—ISOLATED ELEMENTS OF THE MEMBRANOUS LABYRINTH OF VARIOUS VERTEBRATES. (After G. Retzius.)

A, from the macula acustica communis of *Myxine glutinosa*; B, from the macula acustica neglecta of *Raia clavata*; C, from the crista acustica of an ampulla of *Amblystoma*; D, from the crista acustica of the anterior ampulla of *Rana esculenta*.

fz, thread-like cells; *hz*, hair-cells with auditory hairs (*h*); *n*, nerve. On the left side of D the auditory hair has become broken up into its constituent fibres.

In Amphioxus, an auditory organ is wanting. In all Craniates, except Cyclostomes (p. 295), three semicircular canals are present, and these lie in planes roughly at right angles to one another. They are distinguished as the *anterior vertical*, the *posterior vertical*, and the *horizontal* (*external*) *canal* (Fig. 213). The first and last-named arise from the portion of the utriculus known as the recessus utriculi, and at its origin each has a vesicle-like swelling or *ampulla*, enclosing sensory cells. The posterior canal also arises with an ampulla from a prolongation of the utriculus. The other end of the horizontal canal opens by a funnel-shaped enlargement into the utriculus, while that of the anterior and of the posterior canal unite to form a common tube, the so-called *canal commissure* (sinus superior), which also opens into the utriculus.

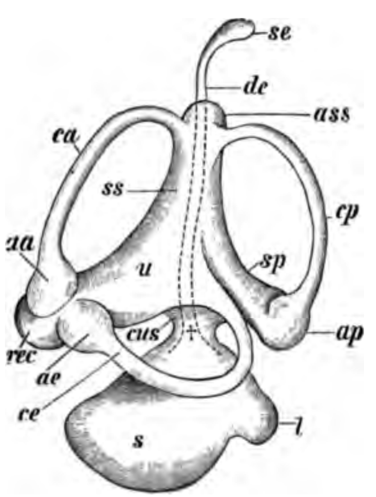

FIG. 213.—SEMIDIAGRAMMATIC FIGURE OF THE LEFT MEMBRANOUS LABYRINTH OF A VERTEBRATE. As seen from the outer side.

ass, apex of the sinus utriculi superior; *ca*, *ce*, *cp*, anterior, external, and posterior semicircular canals; *aa*, *ae*, *ap*, the corresponding ampullæ; *cus*, utriculo-saccular canal; *de*, *se*, ductus and saccus endolymphaticus, the former arising from the sacculus at †; *l*, recessus sacculi (lagena); *rec*, recessus utriculi; *s*, sacculus; *sp*, sinus utriculi posterior; *ss*, sinus utriculi superior; *u*, utriculus.

Concretions composed mainly of carbonate of lime are present in the regions of the various nerve end-plates of the auditory organ in all Vertebrates. These *otoliths*, which arise in the epithelium lining the organ, and are then set free into its cavities, present the greatest variety both in form and size. The largest and most massive ones are seen in Teleosts. They either consist of a single mass or separate otoliths are present in different regions of the labyrinth.

The sensory epithelium, to which the branches of the auditory nerve are distributed, is situated in the following parts of the membranous labyrinth: (1) the three ampullæ of the canals, in each of which the auditory cells are situated on a ridge (*crista acustica*) projecting into the lumen (Fig. 214); (2) the utriculus and the recessus utriculi; (3) the sacculus and lagena, or rudiment of the cochlea; (4) the rudimentary *macula acustica neglecta*, which in Fishes, Birds, and Reptiles is situated on the floor of the utriculus close to the sacculo-utricular canal, in Amphibians on the inner side of the sacculus, and in Mammals undergoes a gradual reduction and may even become obliterated.[1] The several portions of the sensory plate or *macula acustica*, which are originally continuous, become disconnected from one another later, and from Teleosts onwards are seen as separate maculæ acusticæ.

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[1] In addition to these, there is a transitory *macula ductus reunientis* situated in the region of the sacculo-cochlear duct.

A number of the regions characterised by the possession of this sensory epithelium are not concerned with the sense of hearing: those of the ampullæ, for instance, and probably those situated in the utriculus, are to be looked upon as *organs of equilibration*, serving for the orientation of the individual in space. The fact that the above-mentioned parts of the membranous labyrinth are phylogenetically very ancient structures, and also that the organ in Invertebrates to which the function of hearing was formerly ascribed has now been proved to be concerned mainly with equilibration, indicates that the latter function was the primary one in the vertebrate membranous labyrinth. Later, on the gradual appearance of the cochlea, a division of labour took place, the more ancient part of the labyrinth retaining its primitive function, while the new portion by degrees became differentiated into a specialised auditory organ serving for the analysis of sound vibrations.

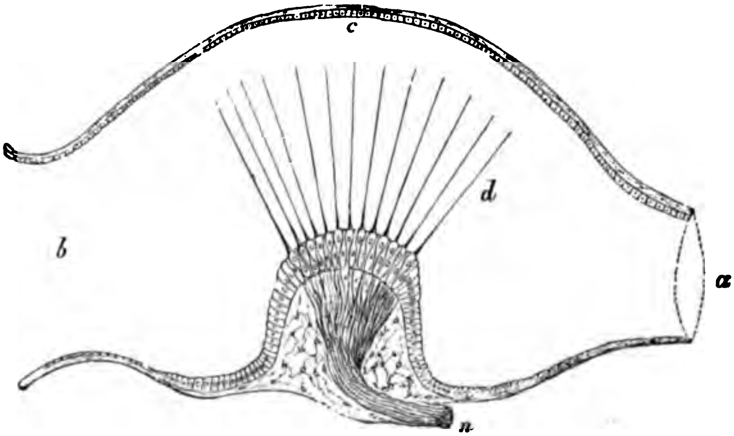

FIG. 214.—LONGITUDINAL SECTION OF AN AMPULLA OF GOBIUS. (After Hensen.)

a, base of semicircular canal; *b*, point of opening of the ampulla into the alveus communis; *c*, epithelium on the wall of the ampulla; *d*, auditory hairs; *n*, nerve passing into the connective-tissue of the crista.

The higher we pass in the Vertebrate series, the greater share does the mesoderm take in the formation of the auditory organ. At first—that is, in Fishes—the auditory capsule lies close to the surface, and is thus easily accessible to the waves of sound, which are conducted partly through the operculum (when present), and partly through the gill-cavities or spiracle. In the higher animals the auditory organ gradually sinks further and further inwards from the surface, so that a new method for conducting the sound-waves to the internal ear is necessary, and certain accessory

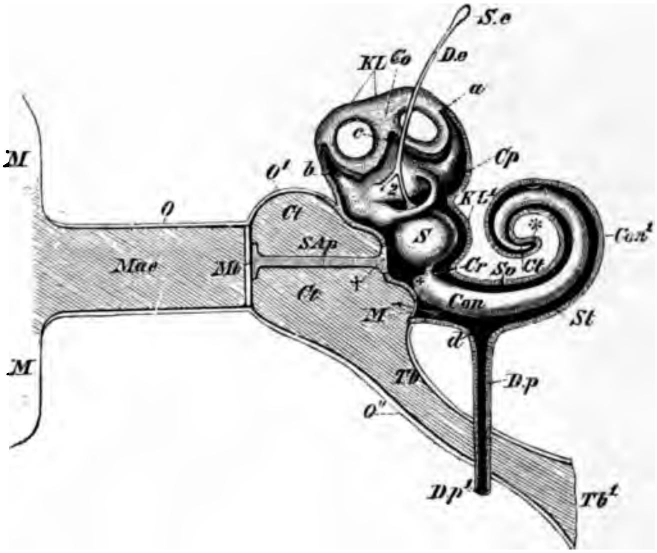

FIG. 215.—DIAGRAM OF THE ENTIRE AUDITORY ORGAN OF MAN.

External Ear.—*Mae*, external auditory meatus; *M*, *M*, pinna; *Mt*, tympanic membrane; *O*, wall of meatus.
Middle Ear.—*Ct*, *Ct*, tympanic cavity; *M*, fenestra rotunda (cochleæ); O^1, wall of tympanic cavity; *O''*, wall of Eustachian tube; *SAp*, sound conducting apparatus, drawn in the form of a rod, representing the auditory ossicles; the point † corresponds to the stapes, inserted into the fenestra ovalis (vestibuli); *Tb*, Eustachian tube; *Tb'*, its opening into the pharynx.
Internal Ear, with the greater part of the bony labyrinth (*KL*, KL^1) removed.—*a*, *b*, the two vertical canals, one of which (*b*) is shown cut through: the horizontal canal is seen between 2 and *S*; *c*, *Co*, commissure of the canals of the membranous and bony labyrinths respectively; *Con*, membranous cochlea, which ends blindly at +; *Con'*, bony cochlea; *Cp*, cavum perilymphaticum; *Cr*, canalis reuniens; *D.p*, ductus perilymphaticus, which arises from the scala tympani at *d*, and opens at $D.p^1$; *S*, sacculus; *S.e*, *D.e*, saccus and ductus endolymphaticus; the latter bifurcates at 2, where its outline should have been dotted, so as to indicate that it opens on the *inner* side of the labyrinth; *Sv* and *St*, scala vestibuli and scala tympani, which at * pass into one another at the cupula terminalis (*Ct*).

structures become developed (Fig. 215). In the first place, a canal, developed in the position of the hyomandibular or spiracular cleft,[1] takes on a close relation to the auditory apparatus, and gives rise to a spacious chamber, the *tympanic cavity* or *middle ear*, communicating with the pharynx by the *Eustachian tube*, and being closed externally by a vibratory *tympanic membrane*, between which and the auditory capsule a sound-conducting apparatus (*columella* or *auditory ossicles*, pp. 98, 133) extends. In higher forms still, the tympanic membrane is situated more deeply at the base of an *external auditory meatus* or *passage*, to which in Reptiles the first indications of a muscular fold of the integument are added. Only in Mammals, however, does the meatus play an important part, and in them a typical *pinna* or *auricula* is developed, which, with the meatus, constitutes what is known as the *external ear*.

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[1] The cavity of the middle ear is doubtless derivable in the first instance from the spiracular cleft which in Elasmobranchs is in close relation to the ear, and thus seems to be particularly well adapted for conducting sound waves. Indications of the former relation of the tympanic cavity with the respiratory function are seen in the Frog, in which the cutaneous branch of the pulmonary artery sends a large branch to its mucous membrane. The morphology of the tympanum itself is not clear, as it is developed secondarily and is apparently not strictly homologous in Anura, Sauropsida, and Mammalia.

Cyclostomes.—In Petromyzon there are only two (vertical) semicircular canals, which unite together in a common section, the so-called commissure; in Myxine only one canal is present, but this, as it possesses two ampullæ, probably represents the two united with one another (Fig. 216, A).

Fishes.—The auditory organ of all true Fishes (Fig. 216, A^1–C) follows the general plan given above, and the same may be said for all the higher Vertebrates. Almost without exception we meet with a division into a *pars superior*—represented by the *utriculus* and *semicircular canals*, which remains essentially much in the condition already described, and a *pars inferior*—constituted by the *sacculus* and *cochlea*, which gradually becomes more differentiated, and attains a higher and higher degree of development and functional perfection. In Fishes, the lagena or cochlea consists simply of a small knob-like appendage of the sacculus, which opens freely into the main cavity of the latter by means of the sacculo-cochlear canal: it is absent in Chimæra. The utriculus and sacculus also communicate with one another by the sacculo-utricular canal.[1] In Elasmobranchs the ductus endolymphaticus opens to the exterior dorsally, and is thus in free communication with the sea-water.[2] In certain Teleosts, in addition to a large otolith situated in the sacculus and smaller ones in the lagena and recessus utriculi respectively, calcareous masses may be present in outgrowths from the sacculus.

In Chimæroids, Ganoids, Teleosts, and Dipnoans the auditory capsules are not completely surrounded by cartilage or bone, the perilymphatic and cranial cavities only being separated by a fibrous partition. As compared with the practically independent carti-

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[1] In Plagiostomes the utriculus and sacculus are not divided off from one another, and the anterior and posterior canals do not unite in a sinus utriculi. In Rays the canals are almost completely circular.

[2] The endolymphatic duct corresponds to the stalk of the auditory vesicle connecting it with its superficial point of origin; in Vertebrates other than Elasmobranchs (except in Teleosts, in which it is wanting) it becomes separated very early from the outer ectoderm.

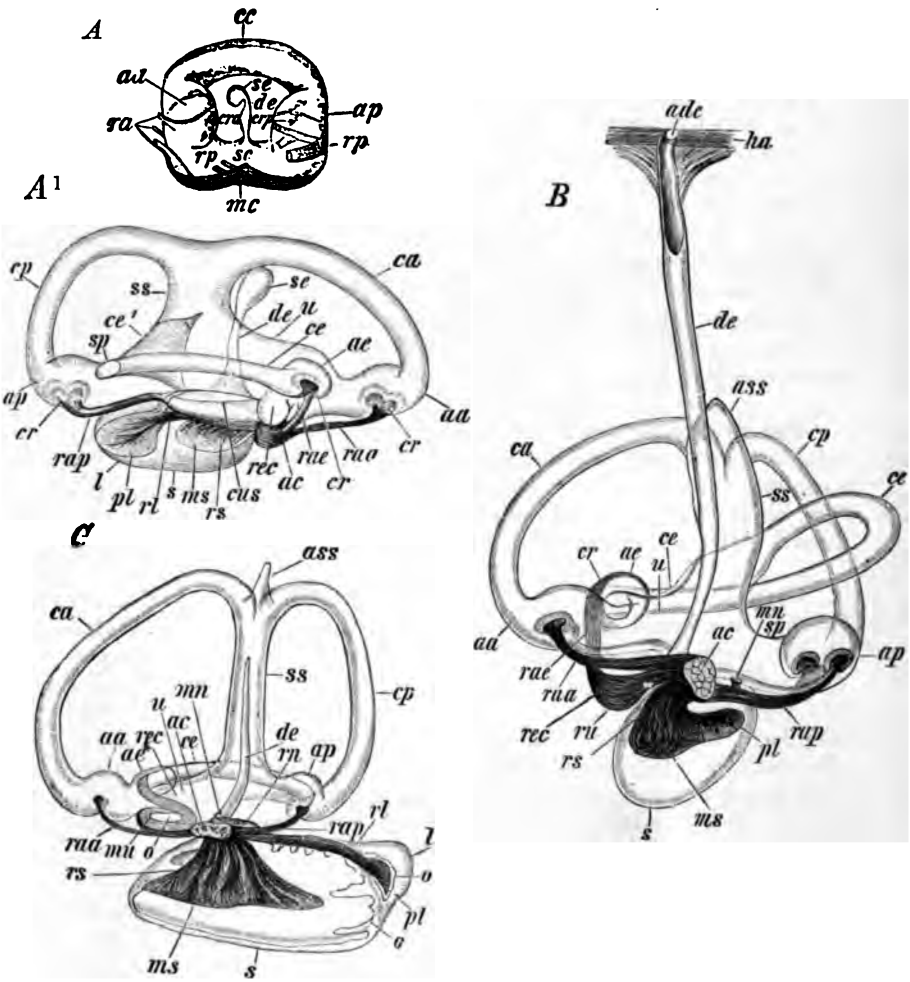

FIG. 216.—MEMBRANOUS LABYRINTH OF VARIOUS FISHES. (After G. Retzius.)
A, *Myxine glutinosa*, from the inner side.

aa, *ap*, anterior and posterior ampulla; *cc*, canalis communis; *de*, ductus endolymphaticus; *cra*, crista acustica of the anterior, and *crp*, of the posterior ampulla; *mc*, macula acustica communis; *ra*, *rp*, anterior and posterior branches of the auditory nerve; *sc*, saccus communis; *se*, saccus endolymphaticus.

A^1, *Acipenser sturio*, from the outer side; B, *Chimæra monstrosa*, from the inner side; C, *Perca fluviatilis*, from the inner side.

aa, *ae*, *ap*, anterior, external, and posterior ampulla; *ac*, auditory nerve; *ass*, apex of the sinus superior; *ca*, *ce*, *cp*, anterior, external (horizontal) and posterior semicircular canals; *cr*, crista acustica of the ampullæ; *cus*, utriculo-saccular canal; *de*, ductus endolymphaticus, which in B opens externally through the skin *ha* at *ade*; *l*, lagena (cochlea); *mn*, macula acustica neglecta; *ms*, macula acustica of the sacculus; *mu*, macula acustica of the recessus utriculi; *o* (in C), otoliths in the recessus utriculi, sacculus, and lagena; *pl*, papilla acustica of the lagena; *raa*, *rae*, *rap*, *ru*, *rs*, *rl*, *rn*, the various branches of the auditory nerve; *rec*, recessus utriculi; *s*, sacculus; *se*, saccus endolymphaticus; *ss*, *sp*, sinus utriculi superior and posterior; *u*, utriculis.

laginous capsules of Cyclostomes, those of Gnathostomes in general became gradually more and more drawn into the skull in the course of development, and on the partial reduction of their cartilage, certain of the cranial bones having primarily no relation to them may take part in enclosing the labyrinth (many Teleosts[1]).

The auditory organ of the Dipnoi most nearly resembles that of Elasmobranchii, and more particularly that of Chimæra. In Protopterus the swollen endolymphatic duct of either side gives rise to a number of tube-like diverticula filled with otolithic substance. These almost entirely cover the fourth ventricle of the brain, and extend backwards as far as the sensory root of the first spinal nerve.

Amphibians.—The membranous labyrinth of Amphibians resembles that of Fishes and Dipnoans in many respects, but important differences are seen—more particularly as regards the lagena, which, especially in the Anura, becomes further constricted off from the sacculus and has close relations to the perilymphatic system, reaching a higher stage of development. The sacculus itself in Anura is considerably reduced, while in Urodeles it is relatively larger than in Fishes.

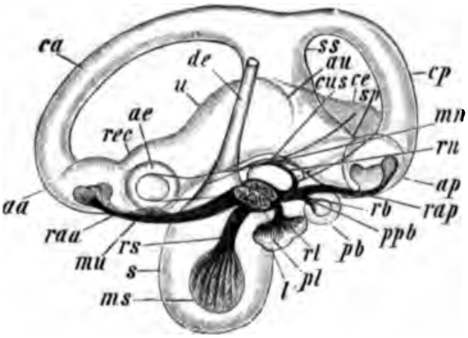

FIG. 217.—RIGHT MEMBRANOUS LABYRINTH OF *Rana esculenta*, from the inner side. (After G. Retzius.)

au, aperture of utriculus; *cus*, utriculo-saccular canal; *l*, lagena cochleæ; *mu*, *ms*, *mn*, macula acustica recessus utriculi, sacculi, and neglecta; *pb*, pars basilaris cochleæ; *pl*, *ppb*, papilla acustica lagenæ and basilaris: *raa*, *rap*, *rs*, *rn*, *rl*, *rb*, branches of auditory nerve to the anterior and posterior ampullæ, sacculus, macula neglecta, lagena, and pars basilaris. (Other letters as in Fig. 216, A¹—C.)

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[1] In certain Teleosts (Siluroidei, Gymnotidæ, Characinidæ, Gymnarchidæ, Cobitidæ, Cyprinoidæ) the auditory organ comes into relation with the air-bladder by means of a chain of bones ("Weberian ossicles") surrounded by a continuation of the dura mater and derived from certain parts of the four anterior vertebræ and corresponding pairs of ribs: it is possible that by this means the relative fulness of the air-bladder can be appreciated by the Fish. Connections between processes of the air-bladder and the internal ear are also met with in several other Teleosts.

The first indications of a *pars basilaris* with its *papilla basilaris lagenæ* are already met with in certain Urodeles, but they lie inside the upper part of the lagena, close to the sacculus.

In the Anura (Figs. 217 and 218) a higher condition is seen in the presence of a peculiar small outgrowth of the thickened wall of the lagena on which a definite region, supported by cartilage, corresponds to the *basilar membrane* of higher types. The lagena and pars basilaris now open close together but independently of one another in the posterior part of the sacculus. Thus, in addition to those present in Fishes, a new patch of nerve-endings is added, viz., the *papilla acustica basilaris lagenæ.*

The ductus endolymphaticus may give rise to large sac-like enlargements containing calcareous matter which meet those of the other side, either on the dorsal surface only, or on both dorsal and ventral surfaces of the brain. The latter is the case in Anura, for instance, in which the sac extends as an unpaired structure along the whole vertebral canal dorsally to the spinal cord, giving rise to paired outgrowths extending through the intervertebral foramina and forming the characteristic *calcareous bodies* situated close to the spinal ganglia. These consist of numerous intercommunicating tubes lined by pavement epithelium and plentifully supplied with capillaries.

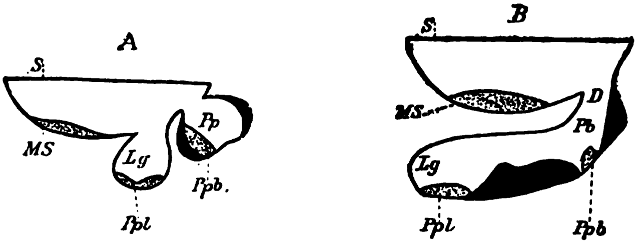

FIG. 218.—DIAGRAM SHOWING THE RELATIONS OF THE LAGENA AND PARS BASILARIS IN ANURA (A) AND SAUROPSIDA (B). The outer wall of the sacculus faces upwards. (After H. Spencer Harrison.)

D, ductus sacculo-cochlearis; *Lg*, lagena; *MS*, macula sacculi; *Pb*, pars basilaris with its cartilaginous framework; *Ppb*, papilla basilaris; *Ppl*, papilla lagenæ; *S*, sacculus.

The perilymphatic cavity of Amphibians communicates medially with the cranial cavity by a *perilymphatic duct*, and the same is true of the Amniota.

A further advance in structure as compared with Fishes is seen in the gradual differentiation of a *middle ear.* In the outer wall of the auditory capsule is a membranous space, the *fenestra vestibuli* (*ovalis*), which is plugged by a cartilaginous *stapedial plate*, and from the latter a rod-like cartilage or bone, the *columella*, usually extends outwards towards the quadrate and paraquadrate (p. 98).

A *tympanic cavity*, with a *tympanic membrane* supported by a ring of cartilage lying on the level of the skin, and a *Eustachian tube* opening into the pharynx, are met with in most Anura,[1] in which also the columella is more perfect, consisting of a bony and cartilaginous rod expanded distally to fit against the tympanic membrane. The columella is wanting in certain Urodeles (*e.g.* Triton). A membranous *fenestra cochleæ* (*rotunda*) in the outer wall of the auditory capsule is present in many Amphibians and in all higher Vertebrates in addition to the fenestra vestibuli. The ear of the Gymnophiona essentially resembles that of the Urodela.

Reptiles and Birds.—In Chelonians, the auditory organ shows many points of resemblance to that of Urodeles; and in all the Sauropsida the chief modifications are confined to the cochlea, which gradually shows a higher condition of development in passing from Chelonians and Snakes to Lizards and Crocodiles.

In Chelonians the lagena and pars basilaris are almost completely united in the cochlea,[2] and, in contrast to the Anura, they now communicate with the sacculus by a single aperture. The cochlea grows out in the form of a short canal ("ductus cochlearis)," which in Crocodiles and Birds is considerably longer and slightly coiled (Figs. 219 and 220). A more marked differentiation also gradually takes place in the membrana basilaris and the papilla acustica basilaris (Fig. 218, B). Both become more and more elongated, and, at the same time, distinct indications of *scalæ tympani* and *vestibuli* are seen (cf. Fig. 223). In the Lacertilia the most varied types of auditory organ are met with, gradually leading up to that seen in the Crocodilia. Thus there is a continuous and an unbroken series from the lower forms to the higher.[3]

Thus the cochlea gradually becomes more independent of the sacculus, which shows the greatest variety both as to form and size in the different types. It is usually very small in Birds, for instance, while in Lizards (*e.g.* Lacerta) it is of considerable size. The aperture of communication between the utriculus and sacculus persists, though it gradually becomes narrowed, as does also that between the sacculus and cochlea. The connection between these latter may be drawn out to form a canal (*canalis reuniens*), and this is particularly the case in Birds; in Crocodiles an intermediate condition between Birds and Lizards is seen. The membranous labyrinth of Birds, however, is always specially characterised by the peculiar arrangement of the anterior and posterior canals, which are greatly arched and the position of their openings into the sinus superior (canal commissure) is reversed. In lower types (Swimming Birds) this peculiarity is less marked than in the higher forms.

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[1] Except, *e.g.* the Pelobatidæ.

[2] At the same time even here a posterior portion (pars basilaris) can be plainly distinguished from an anterior portion (lagena) by a ridge extending into the lumen (*e.g.* Lacerta).

[3] The structure of the auditory organ of Hatteria shows many striking peculiarities: like that of Chamæleo, it occupies an isolated position.

In Chelonians an external and an internal portion of the tympanic cavity can be distinguished: the former is surrounded by the quadrate, which is correspondingly hollowed out and covered externally by the tympanic membrane. The two portions communicate by a canal through which the columella extends, and which is bounded either entirely by the quadrate or partially by soft parts also.

In many Reptiles the distal end of the ductus endolymphaticus is situated close under the roof of the skull beneath the parieto-occipital suture, and in the Ascalabota the duct even leaves the cranial capsule, passes back between the muscles of the neck, and in the region of the pectoral arch becomes swollen to form a large folded sac, from which finger-shaped processes extend to the ventral surface of the vertebral column and to the sub-mucous tissue of the pharynx. These processes may also branch out in a labyrinthic manner into the orbit: they are filled with a white semi-solid mass of otolithic substance, as is the endolymphatic duct of all Vertebrates, at any rate in the embryo. In Birds, the duct does not pass out of the cranial cavity.

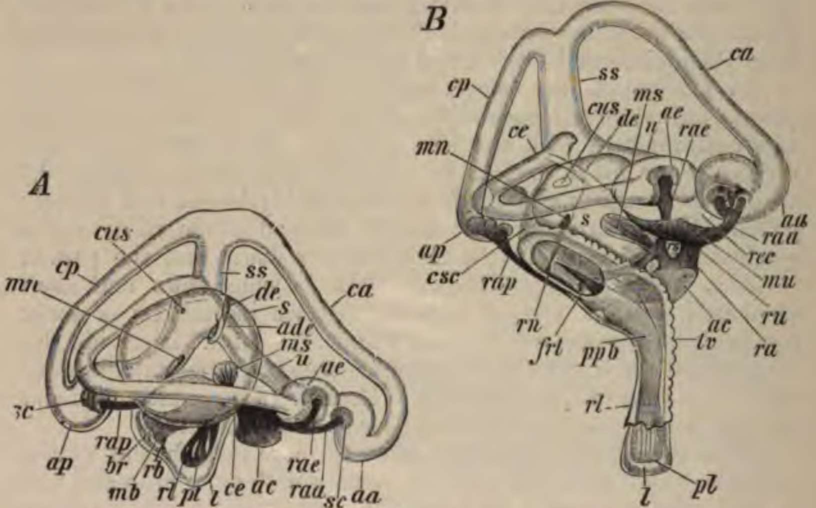

FIG. 219.—RIGHT MEMBRANOUS LABYRINTH OF A, *Lacerta viridis*, AND B, *Alligator mississippiensis*, from the outer side. (After G. Retzius.)

ade, aperture of the ductus endolymphaticus; *csc*, sacculo-cochlear canal; *frt*, foramen recessus scalæ tympani; *mb*, membrana basilaris: *sc*, septum cruciatum; *tv*, tegmentum vasculosum. (Other letters as in Figs. 216 and 217.)

A tympanic membrane is present in Birds and all Reptiles except Hatteria, Snakes, and Amphisbænians, in which the tympanum and Eustachian tube have undergone degeneration.

Especially in Crocodiles and Birds, in which the two Eustachian canals open by a single median aperture into the pharynx,[1] the tympanic cavity is complicated, and is continued into pneumatic cavities in the neighbouring bones. The osseo-cartilaginous columella is well developed in most of the Sauropsida, and is not distinct from the stapedial plate; in Hatteria it is continuous distally with the hyoid (p. 115).

In most Lizards the tympanic membrane is on a level with the skin, but in certain forms (*e.g.* Ascalabota, Lacerta, Monitor) an indication of the development of an external auditory passage is seen, the tympanic membrane being partially covered posteriorly by a small fold of skin, usually enclosing the anterior border of the digastric muscle: in Crocodiles there is a definite integumentary valve moved by muscles (abductor of the mandible, supplied by the facial nerve) and enclosing a dermal bone, and in certain Birds also (*e.g.* Owls) there is a movable valve. The tympanic membrane in Birds is situated some distance from the surface in an external auditory passage, and is stretched on a ring formed by several bones of the skull.

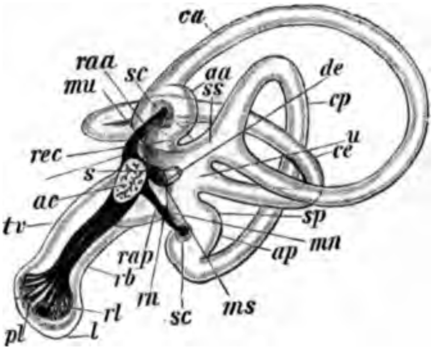

FIG. 220.—RIGHT MEMBRANOUS LABYRINTH OF *Turdus musicus*, from the inner side. (After G. Retzius.) Letters as in previous Figures.

Mammals.—The auditory organ of Mammals reaches a much higher stage of development, but in Monotremes it shows many points of resemblance to that of Reptiles and Birds.

The cochlea now reaches its highest development, and forms a long tube which becomes spirally coiled on itself (Figs. 221 and 222).[2] In this, as well as in the more highly-specialised histological structure of the cochlea, lies the characteristic peculiarity of the auditory organ of Mammals. The auditory nerve forms the axis of the spiral.

In consequence of this development of the cochlea, the papilla basilaris acustica, or, as it is called in Mammals, the *organ of Corti*, is drawn out to a considerable length, and the part of the wall of the cochlea on which it lies is called the ***basilar membrane,*** while the opposite wall is spoken of as the ***membrane of Reissner***

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[1] In Crocodiles this aperture leads into three canals, a median and a paired, all of which communicate with the tympanic cavity in a complicated manner.

[2] In Man it forms nearly three coils, and in other Mammals from one and a half (Cetacea) up to as many as four or more. Thus in the Rabbit there are two and a half, in the Ox three and a half, in the Pig almost four, and in the Cat three coils. The cochlea, as well as the sacculus and all parts of the pars superior of the membranous labyrinth, vary considerably both in form and arrangement in the various types.

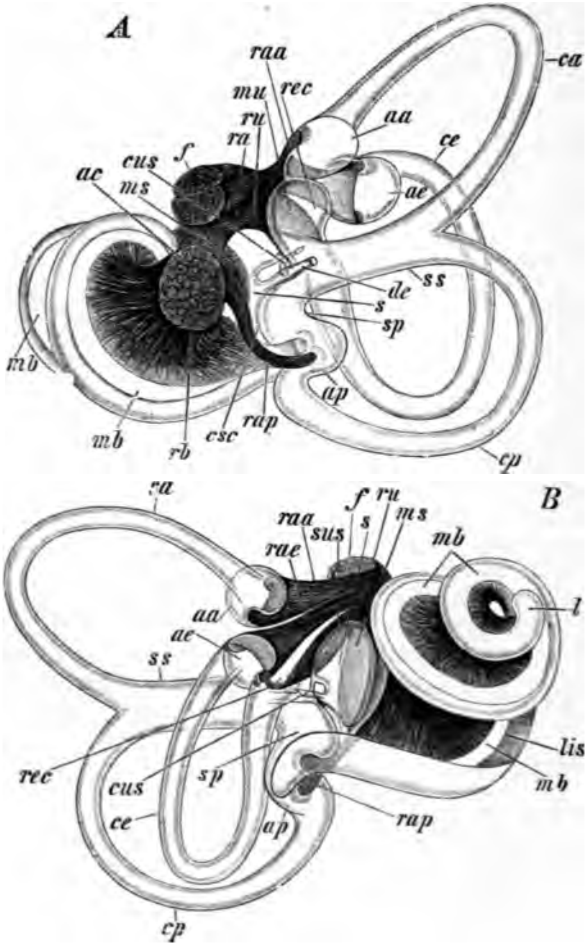

FIG. 221.—RIGHT MEMBRANOUS LABYRINTH OF RABBIT (*Lepus cuniculus*). A, from the inner, and B from the outer side. (After G. Retzius.)

cr, canalis reuniens Henseni; *f*, facial nerve; *lis*, spiral ligament; *mb*, basilar membrane; *rb*, basilar branch of the auditory nerve (*ac*); *sus*, sinus utricularis sacculi. (Other letters as Figs. 216–220.)

(*membrana vestibularis*) (Fig. 223): this is already represented in Reptiles.

Except in Monotremes, the papilla acustica lagenæ has disappeared: thus in other Mammals there remain only six patches of nerve-endings.

The original aperture of communication between the pars superior and pars inferior of the membranous labyrinth—that is, between the sacculus and utriculus, is obliterated in Mammals, the two parts being only indirectly connected with one another by means of the ductus endolymphaticus. This bifurcates at its point of insertion into the membranous labyrinth, one limb being connected with the utriculus and the other with the sacculus (Fig. 215); while its upper end perforates the inner wall of the cartilaginous or bony auditory capsule, passes into the cranial cavity, and terminates by an expanded extremity (*saccus endolymphaticus*) in the dura mater. Osmosis can thus occur between the lymph contained in the endolymphatic and epicerebral lymph-spaces respectively.

The tympanic membrane becomes secondarily situated deep down in the external auditory meatus, and an important difference is thus seen as compared with the Amphibia and most Sauropsida. The tympanic cavity and Eustachian tube are well developed, and in place of a single bony columella there is a chain of three *auditory ossicles*, articulating with one another and extending between the tympanic membrane and the fenestra vestibuli. These are the *malleus*, the *incus* with its orbicular apophysis, and the *stapes*.[1]

Two striated muscles are present in connection with the middle ear. The phyletically older *stapedius* arises from the wall of the tympanic cavity and is inserted into the stapes, serving to keep the membrane of the fenestra vestibuli stretched. It is supplied by the facial nerve and corresponds to the dorsal portion of the deep constrictor inserted on the hyoid in Fishes, from which the hinder belly of the biventer of Mammals also arises. A *tensor tympani*, supplied by the mandibular division of the trigeminal and derived from the system of the adductor mandibulæ (pars pterygoidea),[2] also arises from the wall of the tympanic cavity, and is inserted on to the manubrium of the malleus, serving to stretch the tympanic membrane.

As already mentioned, the form of the membranous labyrinth is repeated by its enclosing cartilaginous or bony capsule, which forms, so to speak, a sort of cast around its individual parts. In Mammals the skeletal labyrinth becomes ossified before any other part of the skull, and is incompletely divided into two parts enclosing the utriculus and sacculus respectively. With the latter part is connected the *bony cochlea*, the axis of which lessens in size from base to apex (Fig. 222), and round it a bony lamella (*lamina spiralis ossea*) winds in a spiral manner; this extends into the cavity of the coils of the cochlea without quite reaching as far as the opposite wall, being continued outwards by two laterally-diverging lamellæ, mentioned above as the basilar membrane and membrane of Reissner; these lie at an angle to one another and correspond to the inner walls of the membranous cochlea (*ductus cochlearis* or *scala media*), which is approximately triangular in transverse section. The outer wall abuts against a portion of the peripheral part of the bony cochlea. It is apparent therefore that the scala media does not by any means fill up the lumen of the bony cochlea, but that a cavity is left on either side of it, corresponding to those already met with in the auditory organ of Birds and known as the *scala vestibuli* and *scala tympani* (Figs. 215 and 223). Both of these are continuous with the perilymphatic space, and, following the direction of the scala media, open into one another at the blind end of the latter. The scala vestibuli is shut off from the tympanic cavity by the membrane of the fenestra vestibuli, to which the stapes is applied externally; the scala tympani is closed by the membrane of the fenestra cochleæ.

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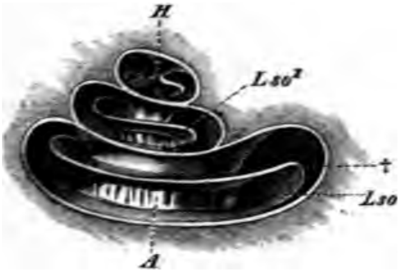
[1] Cf. Fig. 95, in which the mode of development of these parts is shown. There is often also a bony (interhyal) rudiment in the tendon of the stapedius muscle.

[2] In Man the tensor tympani is from the first connected with the tensor veli palatini muscle. In Ornithorhynchus it has a double origin, one part being continuous with the pharyngeal muscles and the other arising independently. A stapedius muscle is wanting in Ornithorhynchus and Echidna, and a tensor tympani in Manis; and in all these three animals the tympanic cavity is subdivided into an upper and a lower portion by a horizontal septum of connective tissue.



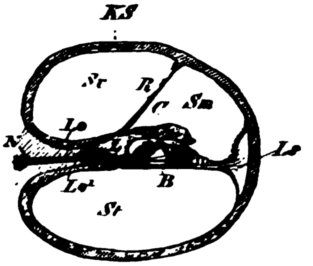


FIG. 222.—BONY COCHLEA OF MAN. (After A. Ecker.)

A, axis; *H*, hamulus; *Lso*, *Lso*¹, lamina spiralis ossea, the free edge of which, perforated by the fibres of the auditory nerve, is visible at †.

FIG. 223.—DIAGRAMMATIC TRANSVERSE SECTION OF THE COCHLEA OF A MAMMAL.

B, membrana basilaris, on which the neuro-epithelium lies; *C*, membrane of Corti; *KS*, bony cochlea; *L*, limbus laminæ spiralis; *Lo*, *Lo*¹, the two layers of the lamina spiralis ossea, between which at *N* the auditory nerve (together with the ganglion, left of *L*) is seen; *Ls*, ligamentum spirale; *R*, Reissner's membrane; *Sm*, scala media (membranous cochlea); *St*, scala tympani; *Sc*, scala vestibula.

On the floor of the bony cochlea, not far from the fenestra cochleæ, is an opening leading into a narrow *ductus perilymphaticus* or *aquæductus cochleæ* (Fig. 215).

The fibres of the auditory nerve running along the axis of the bony cochlea extend in their course laterally outwards, between the two plates of the lamina spiralis ossea (Figs. 223, 224). On the free border of the latter they pass out, and break up into terminal fibrillæ on the inner surface of the basilar membrane. The fibrillæ extend to the sensory or auditory cells, and these are stretched as in a frame between the firm supporting and isolating cells or bacilli. From the surface of the bacilli a resistant net-like membrane (*membrana reticularis*) extends laterally, and through the meshes of the latter the hairs of the auditory-cells project. The auditory cells are covered by a thick and firm membrane —the membrana tectoria *s.* Corti—which perhaps acts as a damper, and which arises from the vestibular lip of the lamina spiralis ossea. The whole extent of the basilar membrane consists of clear, thread-like and very elastic fibres, of which about 16,000 to 20,000 can be made out in Man.

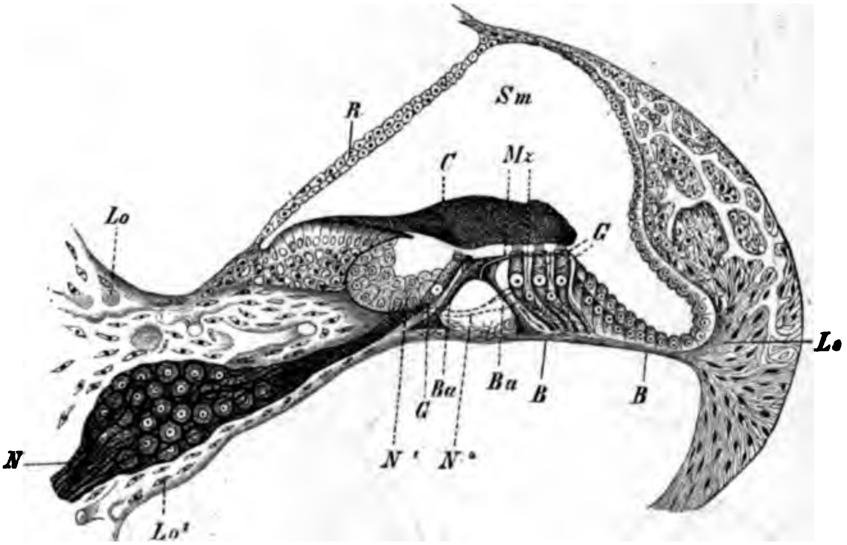


Fig. 224.—The Organ of Corti. (After Lavdowsky.)

B, *B*, basilar membrane; *Ba*, *Ba*, bacilli, or supporting cells; *C*, membrane of Corti; *Lo*, *Lo*¹, the two plates of the lamina spiralis ossea; *Ls*, ligamentum spirale, passing into the basilar membrane; *Mz*, membrana reticularis; *N*, auditory nerve with ganglion; *N*¹, *N*², the nerve branching up into fibrillæ and passing to the auditory cells (*G*, *G*); *R*, membrane of Reissner; *Sm*, scala media.

A true *pinna* or *auricula* (Fig. 225), attached to the border of the external auditory meatus and projecting freely from the head, appears for the first time in Mammals. It is present in Monotremes, and, more especially in Echidna, is in organic connection with the upper end of the hyoid[1] by means of the cartilaginous auditory passage, with which it is continuous. In its formation and further development, the dermal musculature primarily plays the most important part.

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[1] This fact appears to indicate a probable genetic relation between the auricula and the visceral arches.

In the higher Mammals the pinna and the cartilaginous part of

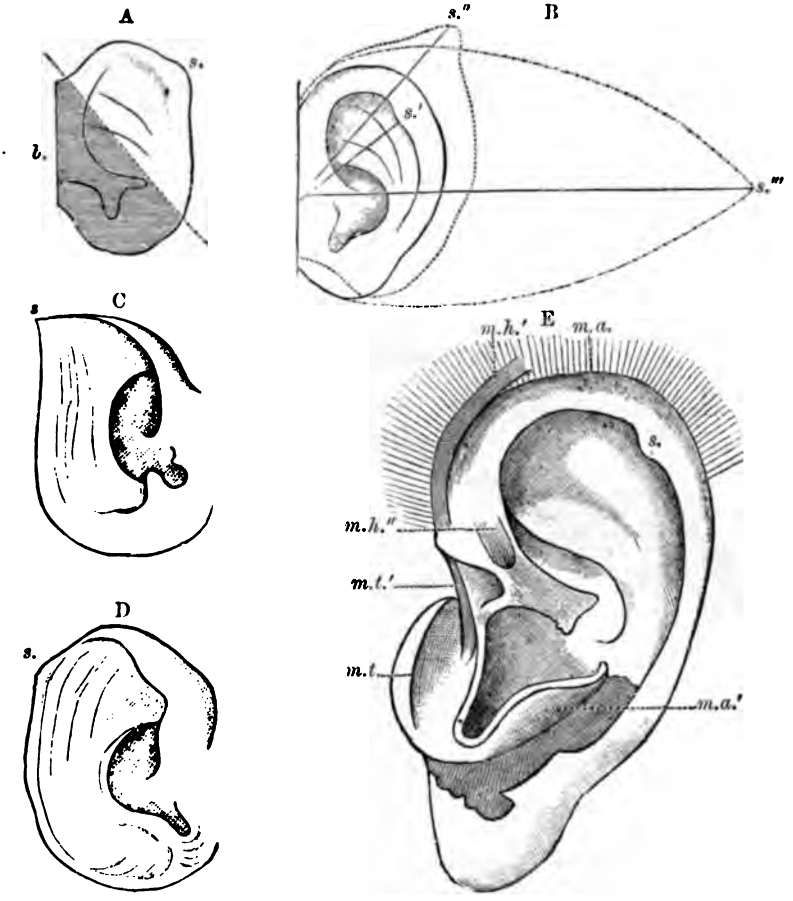

FIG. 225.—THE PINNA OF VARIOUS PRIMATES.

In A, the shaded portion (*b*) represents the zone of the auditory eminences of the embryo, the unshaded that of the later-formed auditory fold. B, Man, Baboon and Ox, drawn to the same scale and superposed: *s'*, *s''*, *s*, spina or tip of the ear. C, Macacus rhesus, with upwardly directed tip; and D, Cercopithecus, with backwardly directed tip. E, Man: the muscles are indicated as follows — *m.a*, attolens auriculæ; *m.a'*, antitragicus; *m.t*, tragicus; *m.t'*, inconstant muscle, extending from the tragicus to the margin of the helix; *m.h'*, helicis major; *m.h''*, helicis minor; *s*, tip of the ear rolled over. A-D, after Schwalbe; E, after Henle.

the external meatus (here also continuous with one another) arise from a series of rounded eminences on the first and second visceral arches, around the hyomandibular (spiracular) cleft, the lower part of which closes up, while the upper part gives rise to the external auditory meatus. These auricular eminences unite to form a nearly continuous ring, on which are later formed the characteristic protuberances known as the *helix*, *antihelix*, *tragus*, and *antitragus*. The variations in form of the pinna which are seen in various Mammals concern essentially the later formed portion (auditory fold), which projects upwards and backwards from the head (Fig. 225).

The muscles which move the ear as a whole, and which are supplied by the facial nerve, include the following in the majority of Mammals: (a) *attrahentes* s. *adductores*, (b) *levatores* s. *attolentes*, (c) *abductores* s. *retrahentes*, (d) *depressores*, and (e) *rotatores*. A gradual reduction of these muscles is seen in the following series: Artiodactyla and Perissodactyla, Canidæ, Felidæ, Prosimii, Primates, the reduction being most marked in Man.[1]

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[1] The auditory fold may undergo marked reduction, *e.g.* in aquatic and subterranean forms. Thus amongst the Pinnipedia, only the Otaridæ possess an "external ear." The corresponding muscles become transformed into sphincters for closing the auditory aperture.

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F. ORGANS OF NUTRITION.

ALIMENTARY CANAL AND ITS APPENDAGES.

The alimentary or enteric canal consists of a tube which begins at the aperture of the *mouth*, passes through the body-cavity (cœlome), and ends at the *vent* or *anus*.[1] The walls of the canal consist of several layers, of which the *mucous membrane*, lining the cavity, and the *muscular layer* external to this, extend throughout the canal. The mucous membrane consists of a superficial *epithelium*, and a deeper *connective tissue layer*, the outer part of which, or *submucosa*, forms a loose network connecting it with the muscular layer.[2] The epithelium is derived from the endoderm, with the exception of that lining the mouth and anus (*stomodæum* and *proctodæum*) which is ectodermic in origin (p. 5). The connective tissue and muscular layers arise from the splanchnic layer of mesoderm of the embryo; and the muscular coat, consisting almost entirely of unstriated fibres, supplied by nerves from the sympathetic system, is, as a rule, divided into two layers, the inner being constituted by circular, and the outer by longitudinal fibres. These serve for the contraction or peristalsis of the wall of the gut, and thus fulfil the double function of bringing the nutritive contents of the latter into the closest possible relation with the whole epithelial surface, and at the same time of removing from the body the substances which have not been absorbed. Striated (voluntary) muscular fibres, supplied by cerebral or spinal nerves, only occur at the anterior and posterior ends of the canal.

An outer accessory *serous* coat, the *peritoneum*, encloses the gut externally in the region of the cœlome. This is covered on its free surface by pavement epithelium, and, dorsally to the alimentary canal, is reflected round the entire body-cavity, converting the

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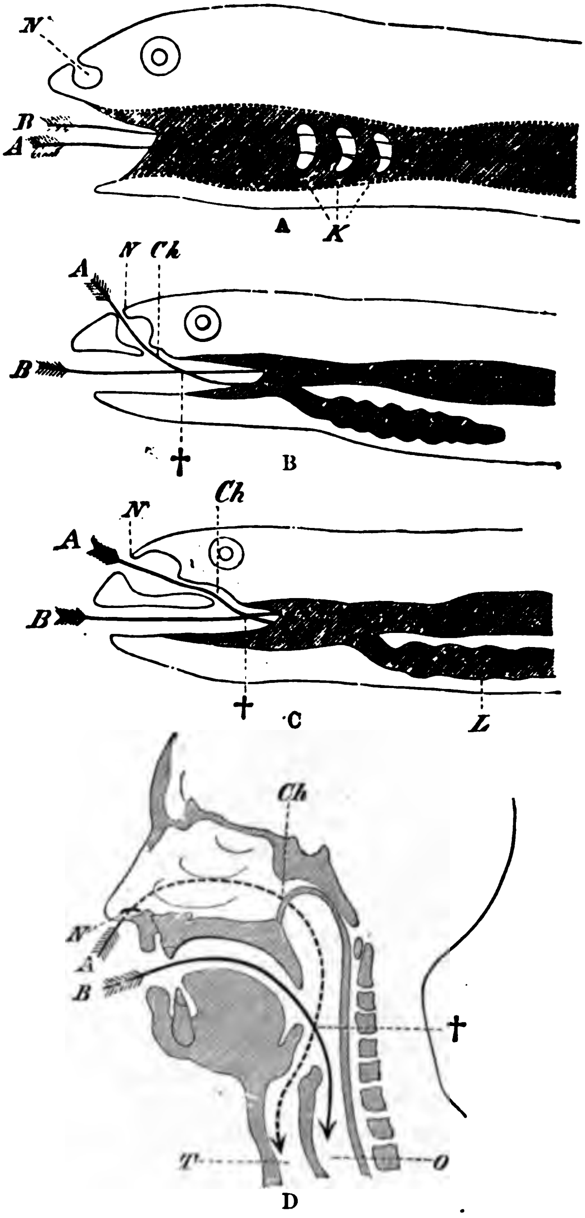
[1] The mouth of Amphioxus apparently corresponds to the first gill-cleft of the left side of craniate embryos (*i.e.* to the left spiracle of Fishes). The mouth of Craniates is probably a new acquisition (*neostoma*, cf. p. 203), which has arisen by the confluence of a pair of gill-clefts. The anus, which in many Vertebrates arises directly from the blastopore, is phylogenetically older than the neostoma.

[2] A layer of smooth muscular fibres may be present in the submucosa, which also encloses lymphoid or adenoid tissue (*solitary follicles*, *Peyer's patches*).



226.—Diagram of the Oral Cavity and Pharynx in a Fish (A), an Amphibian (B), a Reptile (C), and Man (D).

Ch, internal nostril; *D*, alimentary canal; *K*, gill-slits; *L*, lung; *N*, external nostril; *O*, œsophagus; *T*, trachea; the arrow marked *A* indicates the respiratory passage, that marked *B* the nutritive passage; †, the point where the two passages cross one another.

latter into a large lymph-sinus. A *parietal layer*, lining the body-cavity, and a *visceral layer*, reflected over the viscera, can thus be distinguished in the peritoneum (Fig. 10). The region where one passes into the other, which is thus primitively double, is called the *mesentery*,[1] and this serves not only to support the alimentary canal from the dorsal body-wall, but also to conduct the blood-vessels, lymph-vessels, and nerves. With the lengthening of the alimentary canal during development, the mesentery may give rise to a more or less complicated system of folds in which the viscera are enveloped.

The most anterior section of the primitive alimentary tract of the Ichthyopsida serves as a *respiratory cavity* as well as a *food-passage*. A row of sac-like outgrowths, lying one behind the other, are developed in the embryo from the mucous membrane and eventually unite with the ectoderm, apertures being formed to the exterior (Fig. 226, A). In the septa between the channels thus formed, the visceral arches are situated (cf. Fig. 63), and along the septa certain vessels arise by means of which a continual interchange of gases can take place between the blood and the air contained in the water passing through the sacs. In this manner the *gills* or *branchiæ* arise. Even in the Amniota, although gills are not developed, that portion of the cavity of the mouth and pharynx which lies behind the internal nostrils serves as a common passage for air and food unless a proper palate is formed (Fig. 226, B, C).

With the formation of a secondary palate (p. 132), the primitive mouth-cavity becomes divided into an upper *respiratory*, and a lower *nutritive portion*—that is, into a *nasal* and a *secondary* or *definitive mouth-cavity*. The separation, however, is never a complete one, the passage being common to both cavities for a certain region (*pharynx*), which in Mammals is partially separated from the mouth by a muscular fold, the *velum palati*, or free edge of the *soft palate* (Fig. 226, D).[2]

The alimentary canal of Vertebrates is typically divisible into the following principal sections (Fig. 227):—*mouth-* or *oral-cavity*, *pharynx*, *gullet* or *œsophagus*, *stomach*, and *intestine*, the last mentioned being usually differentiated into a *small* and a *large intestine*. The small intestine is in most cases the longest section of the alimentary tract; the bile and pancreatic ducts open into its anterior portion (duodenum).

The large intestine communicates with a *cloaca*, which also receives the urinary and genital ducts, or it may open independently to the exterior. The small intestine may be further differentiated into *duodenum, jejunum* and *ileum,* and the large intestine into *colon* and *rectum.* A *blind-gut* or *cæcum* is often present at the junction of the large and small intestine. Between the stomach

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[1] In Murænoids, Dipnoans and Lepidosteus, a *ventral mesentery* is also present, but in Lepidosteus it only extends for a short distance along the hinder part of the gut.

[2] A membranous velum palati exists in Crocodiles. A median, finger-like process of the soft palate, the *uvula*, is well developed only in Man and some Apes.

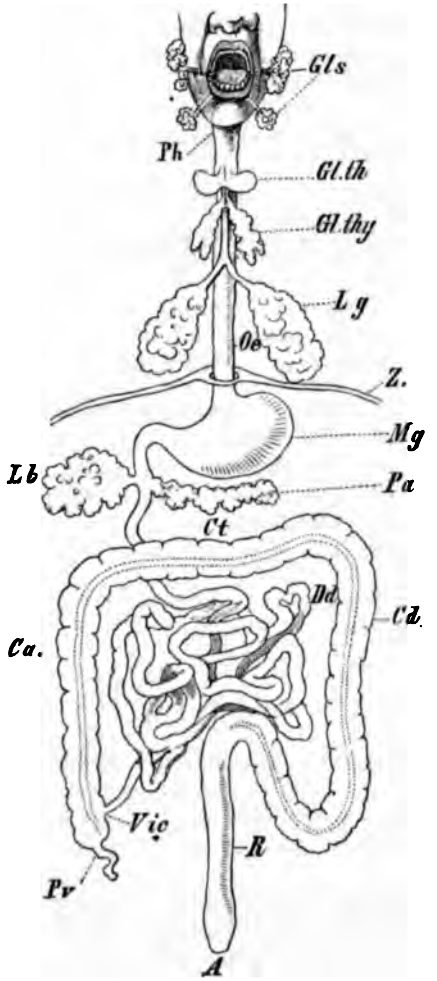

FIG. 227.—DIAGRAM OF THE ALIMENTARY CANAL OF MAN.

A, anus; *Ca, Ct, Cd*, ascending, transverse, and descending portions of the colon: *Dd*, small intestine; *Gls*, salivary glands; *Gl.th*, thyroid; *Gl.thy*, thymus; *Lb*, liver; *Lg*, lung; *Mg*, stomach; *Oe*, œsophagus; *Pa*, pancreas, *Ph*, pharynx; *Pv*, vermiform appendix (cæcum); *R*, rectum; *Vic*, position of ileo-colic valve; *Z*, diaphragm.

and duodenum, as well as between the ileum and large intestine, there is as a rule a marked elevation of the muscular coat serving as a sphincter (*pyloric* and *ileo-colic valves*). These serve not only to prevent the food from passing along the canal in the wrong direction, but also to retain it within the same portion of the canal for a certain time. There is also a sphincter muscle at the anus.

In almost all cases the alimentary canal becomes more or less coiled, and thus presents a greater surface for absorption. As a general rule, it is relatively longer in herbivorous than in carnivorous animals. A considerable increase of surface also commonly results from the elevation of the mucous membrane to form folds, villi, and papillæ.

Certain *appendages* are also present in connection with the alimentary canal. These are all developed primarily from the endoderm and are thus of epithelial origin: mesodermic elements are added to them secondarily. Whether serving as glands or not, they all arise in the same manner as glands.

Beginning from the mouth the following appendicular organs of the alimentary canal may be distinguished (Fig. 227):—

(1) *Mucous* and *salivary glands.*
(2) The *thyroid.*
(3) The *thymus.*
(4) The *swim-bladder* or *lungs.*
(5) The *liver.*
(6) The *pancreas.*

In addition to these, *gastric* and *intestinal glands* are embedded in the wall of the gut.

Oral Cavity.

In Amphioxus and Cyclostomes the aperture of the mouth is surrounded by an oral hood or funnel supported by skeletal parts, which, in the former and in Myxinoids, is edged with tentacles or cirri: all other Vertebrates are provided with an *upper* and a *lower jaw.*[1]

Definite *lips* provided with muscles first appear in Mammals, and are very varied in form. The space between them and the jaws is spoken of as the *vestibulum oris*; this may become extended on either side to form *cheek-pouches,* which serve as food reservoirs (many Monkeys and Rodents).[2] The lips, together with the cheeks and mobile tongue, are important in suction, as well as in articulate speech (Man). Monotremes are the only Mammals in which they are wanting: in them the jaws are covered by a tough, hairless integument, and in Ornithorhynchus somewhat resemble the beak of a Bird.

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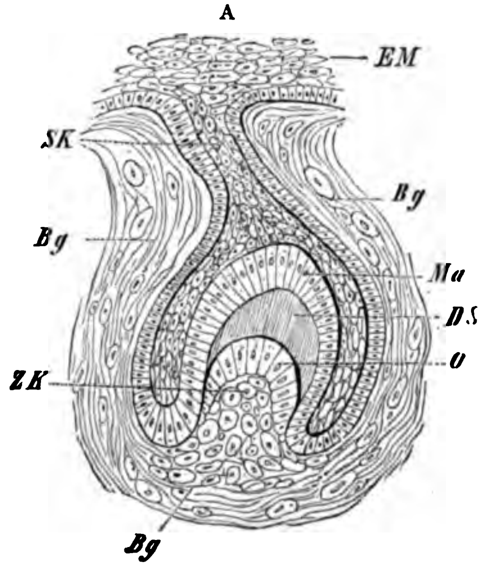
[1] The mouth of the Lamprey serves as a suctorial organ for attaching the animal to foreign objects. The larvæ of Lepidosteus, Polypterus, Lepidosiren, Protopterus, and Anura are temporarily provided with suctorial organs.

[2] Cheek-pouches, opening externally and lined by hair, occur amongst Rodents (Geomyidæ).

The chief organs of the oral cavity are the *teeth*, the *glands*, and the *tongue*.

Teeth.

The teeth are developed quite independently of the endoskeleton, and both ectoderm and mesoderm take part in their formation. The first traces of the teeth are seen primarily in the form of superficial papillæ of the mucous membrane; but secondarily, owing to want of space, the epithelium of the mouth grows inwards so as to give rise to a *dental lamina* which becomes enlarged distally at certain points to form the so-called *enamel-organs*. These, as they grow deeper into the mesoderm, become bell-shaped, and enclose modified masses of connective tissue, the *dental papillæ*; the upper cells of the papillæ, *i.e.* those next to the enamel-organ, are known as *odontoblasts* (Fig. 228). The epithelial and connective tissue germs come into the closest rela-



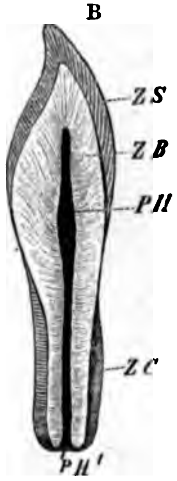


FIG. 228.—DIAGRAM OF THE DEVELOPMENT OF A TOOTH.

Bg, connective tissue follicle or sac surrounding the tooth; *DS*, dentine; *EM*, epithelium of mouth; *Ma*, enamel epithelium; *O*, odontoblasts; *SK*, dental lamina; *ZK*, dental papilla.

FIG. 229.—SEMIDIAGRAMMATIC FIGURE OF A LONGITUDINAL SECTION THROUGH A TOOTH.

*PH*¹, aperture of the pulp-cavity (*PH*); *ZB*, dentine; *ZC*, cement; *ZS*, enamel.

tion with one another, and give rise respectively to the calcified *enamel* with its "cuticula dentis," and to the *dentine*, of which the teeth are composed: the dentine consists of calcified *hard dentine* and vascular *vaso-dentine*. The enamel is the harder and contains little organic matter, and the dentine (ivory) is permeated by a system of fine canals into which delicate processes of the odontoblasts extend. A third, bone-like substance, the *cement*, is also formed from the mesoderm round the bases of the teeth and between the folds of enamel when these are present; it may unite with the bones of the jaw.

The root of the tooth, embedded in the gums, is provided at its lower end with an opening leading into the central *pulp-cavity* (Fig. 229), containing the pulp of the tooth, which consists of cells, blood-vessels, and nerves, and which renders the tooth sensitive.

The form of the teeth is largely dependent on that of the jaws and on the mode of articulation of the latter, as well as on the nature of the food. Functional adaptation may result in complications in the relations of the enamel, dentine, and cement, so as to produce a cutting or grinding surface of different degrees of hardness, and these modifications are generally more marked in the upper than in the lower jaw.

In most Vertebrates below Mammals all the teeth are essentially similar in form (*homodont dentition*): in Mammals, on the other hand, they become differentiated into distinct groups (*heterodont dentition*), viz. into *incisors*, *canines*, and *cheek-teeth* or *grinders* (*premolars* and *molars*).

A succession of teeth takes place throughout life in almost all Vertebrates except Mammals, in which, owing to specialisation, a reduction in the number of tooth-generations has taken place, so that there are practically only two functional sets, the so-called *deciduous* or *milk-teeth* and the *successional teeth*. This difference is expressed by the terms *polyphyodont* and *diphyodont*.

Fishes and Amphibians.—The homology of the teeth and their similarity with the dermal denticles of Elasmobranchs have already been referred to (p. 39). The most primitive form of tooth is that of a simple cone, but even amongst Plagiostomes, in which the teeth are arranged in numerous parallel rows upon the cartilaginous jaws, this form has already become modified in various ways for seizing or crushing the food.

Of those Anamnia which possess a bony skull, four groups of tooth-bearing bones may in general be distinguished, viz. (1) the maxillary arch (*premaxilla* and *maxilla*); (2) the palatal arch (*vomer*, *palatine*, *pterygoid*); (3) the unpaired *parasphenoid*; and (4) the mandibular arch (*dentary* and *splenial*).[1]

True teeth, with enamel, enamel-epithelium, and odontoblasts, are wanting in Cyclostomes, and are represented functionally by a number of conical *horny* teeth, the morphological nature of which has been variously interpreted. Amongst cartilaginious Ganoids teeth are absent in the adult Sturgeon, though present in the embryo. Amongst Teleostei they are wanting in the Lophobranchii, and, except in very early stages, in Coregonus.

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[1] The teeth of Elasmobranchs are comparable to those of the palatal arch and splenial. (For those of Holocephali, cf. p. 88.)

In bony Ganoids and Teleosts, teeth may be present on all the bones bounding the oral cavity, as well as on the hyoid and the branchial arches ("pharyngeal bones.") In the latter position, as well as on the parasphenoid, they often form brush-like groups. In form the teeth may be cylindrical, conical, hooked, or chisel-shaped (Scarus, Sarginæ); in some forms they give rise to a definite pavement, are rounded in form, and serve to crush the food; in others, again, they are delicate and bristle-like (Chætodon), or sabre-shaped (Chauliodus).

In the Dipnoi (Fig. 71) the teeth, which are wanting in enamel (though an enamel organ is present in the embryo Lepidosiren), are exceedingly massive, presenting sharp edges and points: they have probably arisen by the concrescence of a number of individual teeth.[1] More particularly in Ceratodus, the origin of the vomer, palatopterygoid, and dental plates of the mandible from a fusion of the bony basal portions of the teeth is very evident, and the same has been shown in the case of the Amphibia.

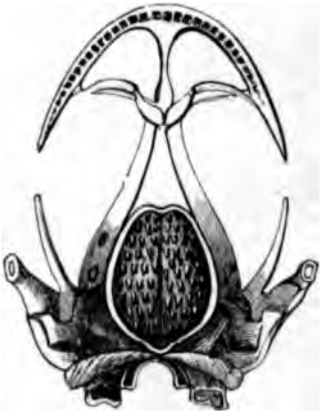

FIG. 230.—SKULL OF *Batrachoseps attenuatus*. From the ventral side, showing the teeth on the parasphenoid.

In the Amphibia there is in general a considerable diminution in the number of teeth as compared with Fishes; and at the same time a much more uniform character is noticeable in their form throughout (Fig. 231, A, B). They are conical, enlarged below, and rest on a definite base, while above they become narrower and slightly curved, ending either in a double (Myctodera, Anura), or a single apex (Perennibranchiata, Derotremata, Gymnophiona); the latter is the more primitive condition. The teeth lie deeply embedded in the mucous membrane, and are present, as a rule, on the premaxilla, maxilla, and mandible (except in Anura), as well as on the vomer and palatine, but rarely on the parasphenoid (*e.g.*

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[1] There are no indications of a succession of teeth in the Dipnoi. In Protopterus the teeth are covered by an epithelial horny layer during the torpid period. The formation of complex teeth by concrescence is apparently not so frequent amongst Vertebrates as was formerly supposed, and does not apply, *e.g.* to those of various Elasmobranchs, of Labyrinthodonts, Ichthyosaurians, and probably also to the mammalian molars.

Spelerpes, Plethodon, Batrachoseps, Fig. 230); in the larvæ of Salamanders and in Proteus the splenial of the lower jaw is also toothed. *Horny teeth* and *horny jaws* are present in larval Anura (except Xenopus), and similar structures occur in Siren lacertina. Teeth are altogether absent in the Bufonidæ and in Pipa.

The teeth of certain of the Stegocephali (Labyrinthodonta) were extremely complicated, the enamel forming numerous corrugated folds extending from the periphery towards the centre.

Reptiles and Birds.—Corresponding with the greater firmness of the skull in Reptiles, the teeth are usually strongly

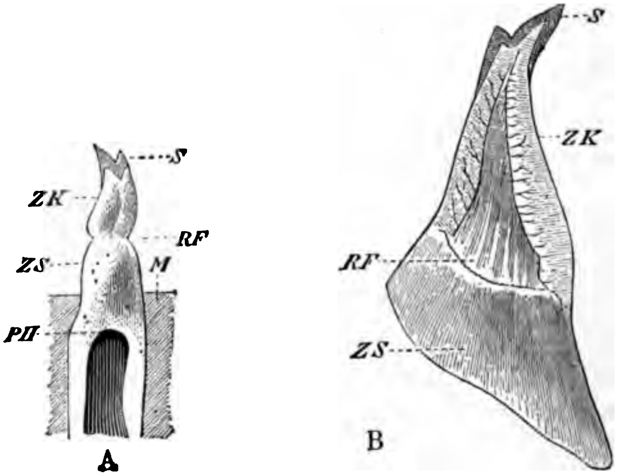

FIG. 231, A—TOOTH OF FROG, and B—OF *Salamandra atra.*

M, maxilla; *PH*, pulp-cavity; *RF*, circular furrow; *S*, apex, covered with enamel; *ZK*, crown; *ZS*, base.

developed, and may be more highly differentiated than in Amphibians. They are either situated upon a ledge on the inner side of the lower jaw, with which their bases become fused (*pleurodont* dentition—most Lacertilia); or they lie on the free upper border of the jaw (*acrodont* dentition—Chameleon); or finally, as in Crocodiles and numerous fossil Reptiles, they are lodged in alveoli (*thecodont* dentition) (Fig. 232). Both upper and lower jaws, and occasionally the palatine and pterygoid also, are toothed (Lizards and Snakes); and in Hatteria, vomerine teeth may also be present. The teeth are usually conical, more or less pointed (Fig. 232, B), and often long and recurved, for seizing the prey (*e.g.* Snakes): in Lizards the apex may be double, and in many Reptiles (*e.g.* Uromastix spinipes, Agamæ, and numerous fossil forms) a heterodont dentition appears to be indicated.[1] In spite of the great modifications which have taken place in the palate of Crocodiles, their teeth, which have a conical form, show the least amount of differentiation in the course of their phylogenetic history. Almost all Reptiles are polyphyodont, but in some cases certain of the teeth are not replaced (*e.g.* Agama colonorum), and in others some of them undergo reduction (*e.g.* Typhlopidæ).

In poisonous Snakes a varying number of maxillary teeth are differentiated to form *poison-fangs*, which, like those of the lower jaw of the poisonous Lizard, Heloderma, are longitudinally grooved anteriorly. In the Viperine forms there are on each side a number of poison-fangs arranged in rows; the stronger ones project freely, while the lesser, reserve teeth lie within the gum (Fig. 233, A); only one of these teeth, however, is firmly fixed to the maxilla at a time. Each fang is perforated by a poison-canal formed by the meeting of the edges of the longitudinal groove, and is incompletely surrounded by the pulp-cavity, the latter having the form of a half-ring in transverse section (Fig. 233, B, C,): the duct of the poison-gland passes into an aperture at the base of the tooth which leads into the poison-canal, and the latter opens by a slit at a short distance from the apex of the tooth on the premaxilla (Fig. 233, A).[2]

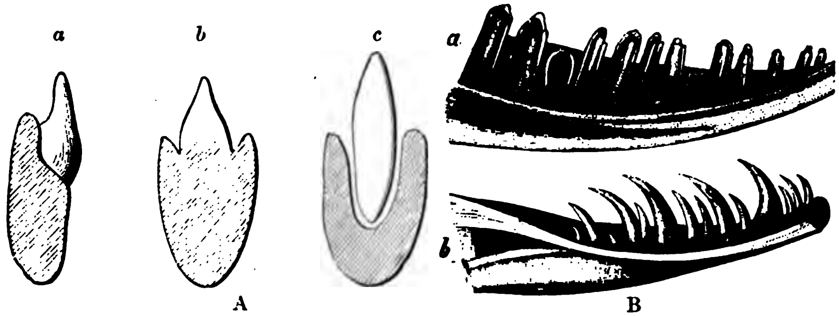

Fig. 232.—A, Diagrammatic Transverse Sections through the Jaws of Reptiles, showing Pleurodont (*a*), Acrodont (*b*), and Thecodont (*c*) Dentitions. B, *a*, Lower Jaw of *Zootoca vivipara*, and *b*, of *Anguis fragilis*. (After Leydig.)

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[1] The teeth of Hatteria are at first simple in form and their attachment is acrodont; the apparent heterodont condition in the adult is due to the fusion of more than one generation of teeth to the bone, which embraces them basally and grows down beyond the gums. In this animal, the vomerine teeth are in the course of suppression; they are usually absent, but may occur on one or both vomers. Functionless teeth are present in the embryo which later disappear, and the same is true of Crocodilus porosus and Iguana tuberculata.

[2] A peculiar, broad, lancet-like tooth, originally paired, is present in embryos of Lizards and some Snakes. It projects considerably beyond its neighbours in the median line of the snout, and serves the young as a means of breaking through the parchment-like egg-shell. This must not be confounded with the analogous structure present in Rana opisthodon or with the horny "neb" in Hatteria, Crocodiles, Chelonians, Birds, and Monotremes, which is purely of an epithelial nature.

Chelonians, like existing Birds, are provided with horny sheaths to the jaws instead of teeth. The presence of teeth in the embryo of Trionyx, as well as of a vestigial dental lamina in embryos of Chelone and certain Birds, proves, however, that this is only a secondary condition. Moreover, in the Cretaceous Birds of N. America (*Odontornithes*) teeth were present, and were either situated in definite alveoli (Ichthyornis), or simply in grooves (Hesperornis). The premaxillæ were toothless, and seem to have possessed a horny beak. The single-pointed teeth of Archæopteryx were probably situated in alveoli.

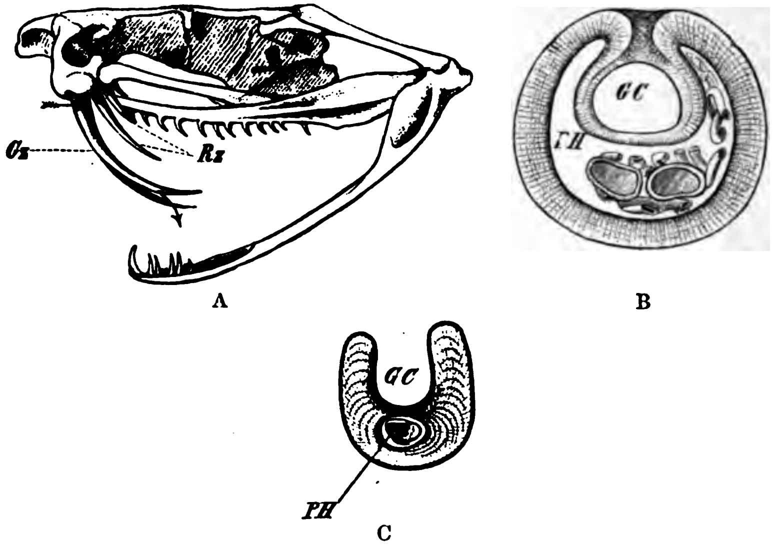

Fig. 233.—Poison-Fangs of a Viperine Snake.

A, skull of Rattlesnake ; B, transverse section through about the middle of the poison-fang of *Vipera ammodytes* ; C, transverse section through the poison-fang of *Vipera ammodytes* near its distal end. (B and C after Leydig.)

GC, poison-canal ; *Gz*, poison-fang ; *PH*, pulp-cavity ; *Rz*, reserve fangs.

Mammals.

In Mammals, a shortening of the jaws, which results in an increase in their power and a diminution in the number of teeth, has taken place along with a higher differentiation of the individual tooth and a reduction in the number of tooth-generations. The heterodont condition which characterises Mammals, as a whole, has arisen from a more primitive homodont condition, and the teeth have become adapted in various ways in correspondence with the method of taking in and biting or masticating various kinds of food. The frequent presence of vestigial, functionless teeth shows that a diminution in number has taken place in the course of time,[1] and such reduction is more marked in the lower than in the upper jaw. An increase in number, on the other hand, such as is met with in Toothed Whales, is due to a secondary differentiation, during ontogeny, of primarily multicuspidate teeth, and the homodont dentition and conical form of the teeth in these Mammals is therefore a specialised and not a primitive condition.

As already mentioned, the succession is nearly always limited to two functional sets, the so-called *deciduous* or *milk*-teeth, and the *successional* or *permanent teeth*, and in many cases even one of these may be vestigial.[2] The milk-teeth represent a historically older generation than the successional teeth: they, however, show numerous adaptations and modifications, and may even be retained in the adult permanently (*e.g.* Marsupials) or for a considerable time (*e.g.* Chrysochloris, certain Centetidæ). Traces of a still earlier set occasionally occur—most frequently and distinctly in the more primitive orders (*e.g.* Marsupials, Insectivores, Rodents): this may be spoken of as a *prelacteal* dentition. As occasionally also certain teeth appear which replace the corresponding "permanent" teeth, indications of at least four sets can be recognised in Mammals.[3]

In each of the two functional sets, *incisors*, *canines*, and *cheek-teeth* or *grinders*, can as a general rule be distinguished. The teeth which replace the milk-grinders are distinguished as *premolars;* the *molars* are situated further back in the jaw and have no predecessors.[4] The latter may therefore be considered as belonging primarily to the milk-series; or more probably they arise from germs, which, owing to an abbreviation of development, really represent more than one set.

All the teeth are embedded in well-developed alveoli of the jaw-bones, the upper incisors being situated in the premaxillæ, the upper canines and cheek-teeth in the maxillæ, and the lower teeth in the dentary. The canine, which corresponds to a specially differentiated premolar and is most characteristically developed in Carnivora, is approximated to the incisors and forms a more or less continuous series with them. The premolars follow behind

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[1] The last molar of Man, or so-called "wisdom-tooth," for instance, seems to be gradually disappearing; it appears last, is usually lost first, and often does not reach the grinding surface.

[2] Thus in the Hedgehog, which presents an intermediate stage between the diphyodont and monophyodont conditions, and also in the Mole and certain Rodents, the milk-dentition is partially reduced. In Scalops and Condylura also most of or all the milk-teeth become absorbed without cutting the gum, and a similar condition is seen in the Pinnipedia, in which, however, they may not be shed until shortly after birth. Thus the succession may take place in the fœtus, so that the milk-teeth are functionless. This is also the case in certain Bats, while in others the milk-teeth may be retained in order to hold the young fast to the teats, and they thus form an interesting example of the retention of organs owing to a change of function.

[3] Thus the polyphyodontism of the lower Vertebrates is replaced in certain Reptiles by an oligophyodont condition, and this again, by the diphyodontism of Mammals, which, by higher differentiation of the individual teeth, may lead to a monophyodont condition.

[4] It must, however, be remembered that in some cases the so-called premolars have no predecessors, and therefore apparently belong to the milk-dentition. Moreover, in Toothed Whales the persistent "milk-teeth" are said to include representatives of an earlier and a later generation, and the same applies to the Manatee.

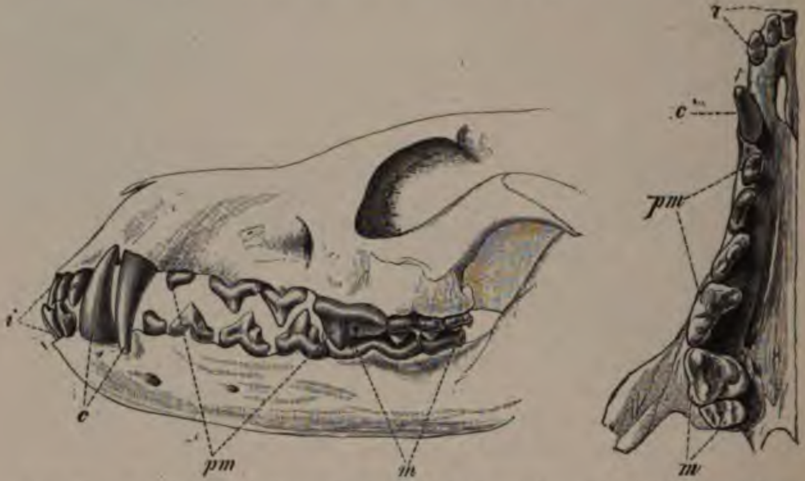

Fig. 234, A.—Teeth of Dog (*Canis familiaris*). The teeth of both jaws from the side, and those of the upper jaw from below.

i, incisors ; *c*, canines ; *pm*, premolars ; *m*, molars.

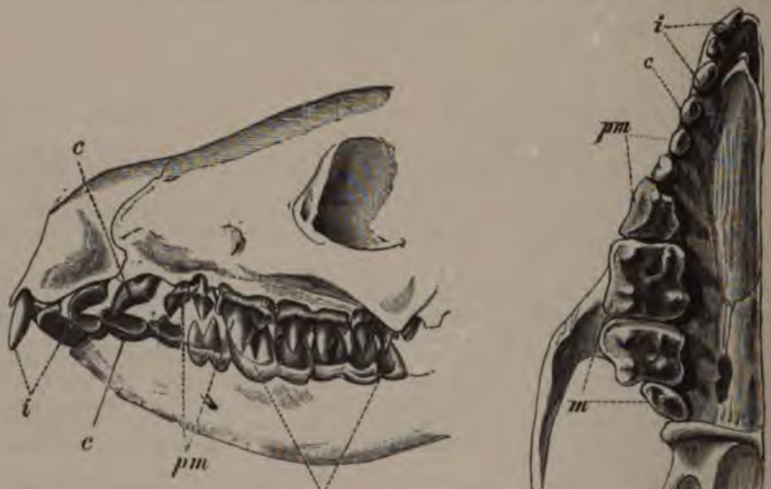

Fig. 234, B.—Teeth of Hedgehog (*Erinaceus europæus*).

the canine, the space often existing between them being called the *diastema*, and then come the molars. The primary arrangement of the teeth is such that there is an alternation between those of the upper and lower jaw: thus the teeth in one jaw do not usually correspond in position with those of the other, but with the interspaces between them.

In some cases the enamel-organ, with its dental papilla, persists in all the teeth, which then continue to grow throughout life (*e.g.* Lepus); in others this is true of the incisors only (*e.g.* Elephant, numerous Rodents, Fig. 237); but more usually growth ceases after a certain time, and the teeth then form definite *fangs* or *roots*, perforated by a small canal communicating with the reduced pulp-cavity.

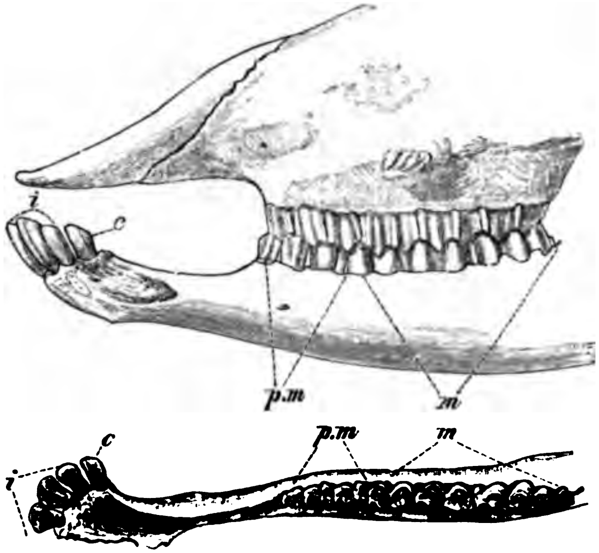

FIG. 235.—TEETH OF SHEEP (*Ovis aries*).

(References as before, but the teeth of the lower instead of the upper jaw are figured from the surface.)

The incisors are usually chisel-shaped, while the canines, in those cases where they are most characteristically developed (Carnivora), possess a pointed, conical form, and are more or less curved. The cheek-teeth either have sharp, cutting crowns (*secodont*, *e.g.* Carnivora), or may possess infoldings of the enamel, or tubercles, the crowns being broad and more or less flat, and adapted for grinding the food. If the tubercles are conical, the tooth is described as *bunodont* (*e.g.* Pig, Hippopotamus), and if crescentic, *selenodont* (*e.g.* Horse, Ruminants): in these cases the relations of the enamel, dentine, and cement are such as to produce an uneven surface with wear, showing a characteristic pattern in the different groups (cf. Figs. 234–236).

The relations and number of the tubercles, as well as the form of the teeth in general, are of great importance in elucidating the ancestral history of the Mammalia, and attempts have been made to trace the evolution of the various forms of molar met with in the Class. According to one view, the tuberculated molar has arisen by the gradual modification of a single conical tooth, which has produced lateral outgrowths or buds. Thus taking a simple conical form as the most primitive type of mammalian tooth, we find that certain extinct Mammals (*e.g.* Triconodon) possessed teeth with a main cone and two lateral cusps. It has been supposed that the more complicated forms have been derived from this *triconodont* tooth—firstly by a rotation of the lateral cusps outwards in the upper, and inwards in the lower one, thus forming a *tritubercular* tooth, with three cusps arranged in a triangle; and secondly by the addition of accessory cusps (the first to appear being the posterior heel or talon), as well as of connecting ridges.[1]

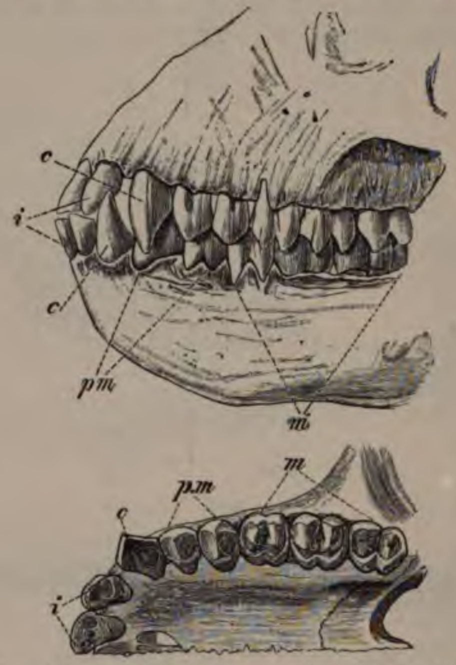

FIG. 236.—TEETH OF A CATARRHINE MONKEY (*Nasalis larvatus*). References as before.

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[1] According to another hypothesis, the mammalian cheek-teeth were primarily multitubercular, having originated by the fusion of a number of simple conical teeth; and certain facts in their development and the presence of multituberculate Mammals in the Triassic rocks indicate that in some cases, at any rate, *they may have* become evolved in this manner.

The Marsupials form a marked contrast to those Mammals referred to on p. 319 in which the milk-dentition has undergone reduction, for in them there is only one functional successional tooth, the fourth premolar, all the others belonging to the milk series. Bud-like enamel-germs occur, however, near all the persistent teeth anterior to the third molar, and these must be looked upon as rudiments of potential teeth and not as vestiges which have become functionless.

In Ornithorhynchus, in which there are indications that two dentinal series are represented, the three multitubercular teeth present on either side of the upper and lower jaws become replaced functionally after a time by the development of horny masticatory plates,[1] and in Echidna they are wanting altogether, the dental lamina undergoing reduction at an early stage. Adult Whalebone-Whales and certain Edentates (Myrmecophaga, Manis) are toothless, but vestiges of teeth occur in the embryo. In other Edentates the teeth are wanting in enamel. Canines are absent in certain Mammals (*e.g.* Rodents), and the incisors may also be wanting. In the typical Ruminants functional incisors and canines are present in the lower jaw only, though tooth-vestiges occur in the premaxillary region of the embryo and occasionally upper canines persist in the adult.[2]

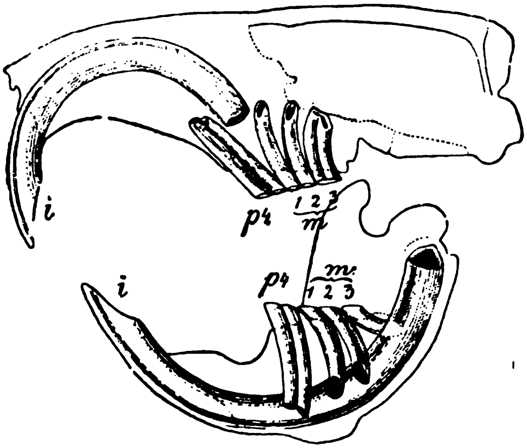

FIG. 237.—OUTLINE OF THE SKULL OF GEOMYS, SHOWING THE RELATIONS OF THE TEETH (after V. Bailey).
i, incisors (which in Rodents correspond to the second incisors of other Mammals); p^4, premolars; *m*, 1, 2 3, molars.

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[1] Horny crushing plates are also present in the Sirenia, the existing forms of which possess numerous teeth, while the extinct Rhytina was toothless.

[2] In the Manatee, the dentition is very peculiar. Traces of incisors, canines, and premolars occur in the embryo, but the adult possesses molars only, which undergo a constant succession from behind throughout life as the anterior ones are pressed forward and fall out; there may be as many as 8—10 functional at the same time. In the Elephant there is also a similar succession of molars, but it is here limited to six.

Sexual differences in dentition exist in a number of Mammals. Thus in Apes the canines and first premolars are more strongly developed in the male than in the female. In the male Wild Boar, Narwhal (Monodon), Dugong (Halicore), and Musk-deer a modification of certain of the teeth (the canines or the incisors) to form *tusks* occurs, and these serve as fighting weapons. In the Elephant and Walrus tusks are present in both sexes: in the former they correspond to incisors, and in the latter to canines. In Elephas antiquus they were relatively enormous.

In describing the teeth of a Mammal it is convenient to make use of a *dental formula* in which their number and arrangement can be seen at a glance, the teeth of one side only being represented. Thus the adult dental formula of those animals, the teeth of which are represented in Figs. 234 to 237, would be :—

Fig. 234, A Dog, $\frac{3 \cdot 1 \cdot 4 \cdot 2}{3 \cdot 1 \cdot 4 \cdot 3} = 42$
„ 234, B Hedgehog $\frac{3 \cdot 1 \cdot 3 \cdot 3}{2 \cdot 1 \cdot 2 \cdot 3} = 36$
„ 235. Sheep, $\frac{0 \cdot 0 \cdot 3 \cdot 3}{3 \cdot 1 \cdot 3 \cdot 3} = 32$
„ 236. Catarrhine Monkey, $\frac{2 \cdot 1 \cdot 2 \cdot 3}{2 \cdot 1 \cdot 2 \cdot 3} = 32$
„ 237. Geomys, $\frac{1 \cdot 0 \cdot 1 \cdot 3}{1 \cdot 0 \cdot 1 \cdot 3} = 20$

The most complete dentition is seen amongst Marsupials, the dental formula of Myrmecobius being $\frac{4 \cdot 1 \cdot 3 \cdot 5 \text{ or } 6}{3 \cdot 1 \cdot 3 \cdot 5 \text{ or } 6} = 52\text{—}54$. The more typical arrangement is $\frac{3 \cdot 1 \cdot 4 \cdot 3}{3 \cdot 1 \cdot 4 \cdot 3} = 44$.

Glands of the Mouth.

The glands of the mouth, like those of the orbit and integument, appear first in terrestrial Vertebrates, that is from Amphibians onwards.[1] They have the function of keeping moist the mucous membrane which comes into contact with the outer air. From being at first almost entirely unspecialised, and giving rise simply to a slimy fluid, they become differentiated later into structures the secretions of which take on a very important function in relation to digestion; they may also, as in the case of poisonous Snakes and Lizards, constitute dangerous weapons of offence.

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[1] A paired glandular organ (so-called "salivary gland") is present in Petromyzon between the mouth and first pair of gill apertures, towards the ventral side. It is surrounded by muscles, apparently produces a fatty secretion, and opens into the mouth.

With their increasing physiological importance a greater morphological complication both as regards number and arrangement takes place. Their histological character also undergoes changes, so that the most varied forms of glands may be recognised.

Amphibians.—With the exception of the Perennibranchiata Derotremata, and Gymnophiona, a tubular gland becomes developed in all Amphibia from the anterior portion of the roof of the mouth (cf. Fig. 193), the main mass of which in Urodeles lies in the cavity of the nasal septum or premaxilla (*intermaxillary* or *internasal gland*). In Anura its position is more anterior than in the Urodela, and it is more largely developed; but in both cases the ducts open into the anterior part of the mouth. In Anura there is a second gland (*pharyngeal gland*) present in the region of the internal nostrils, the secretion of which passes partly into the latter and partly into the pharynx. Numerous gland-tubes are also present in the tongue of Amphibians, and in the Gymnophiona oral glands are abundant.

Reptiles.—The oral glands in Reptilia show an advance on those of Amphibia in being separated into groups. Thus not only is there a *palatine gland*, homologous with the intermaxillary gland, but *lingual*[1] and *sublingual*, as well as upper and lower *labial glands* are present. Chameleons and Snakes are distinguished by a remarkable richness in glands, which are most specialised into definite groups in the latter.

In poisonous Snakes the *poison-gland* becomes differentiated from a portion of the upper labial gland. It is tubular in structure, is enclosed in a strong fibrous sheath, and is acted upon by powerful muscles, so that its secretion can be poured with great force into the duct and thence into the poison-fang (Figs. 233 and 238). The sheath of the poison-gland is formed by a pocket-like enlargement of the zygomatic ligament, and is compressed by the muscles of the jaws. When the Snake strikes, the lower jaw is depressed to its fullest extent and the quadrate, pterygoid, palatine, and transpalatine are pushed forwards by the contraction of the posterior pterygo-sphenoid and pterygo-parietal muscles, thus causing the maxilla to move on its articulation with the prefrontal and to erect the fang. The upper jaw is again brought into its position of rest by the contraction of the anterior pterygo-sphenoidal and transverso-maxillo-pterygo-mandibular muscles.

The sublingual gland of a Mexican Lizard, Heloderma, is also of poisonous nature. The secretion passes out through four ducts, which perforate the bones of the lower jaw in front of the grooved teeth (p. 317).

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[1] In Lacerta, Anguis, and Pseudopus there are numerous depressions of the lingual epithelium lined by goblet cells, which, however, are not differentiated into definite compound glands.

In marine Chelonians and Crocodiles there are no large glands united into groups connected with the mouth, but in Testudo græca there are well developed sublingual glands.

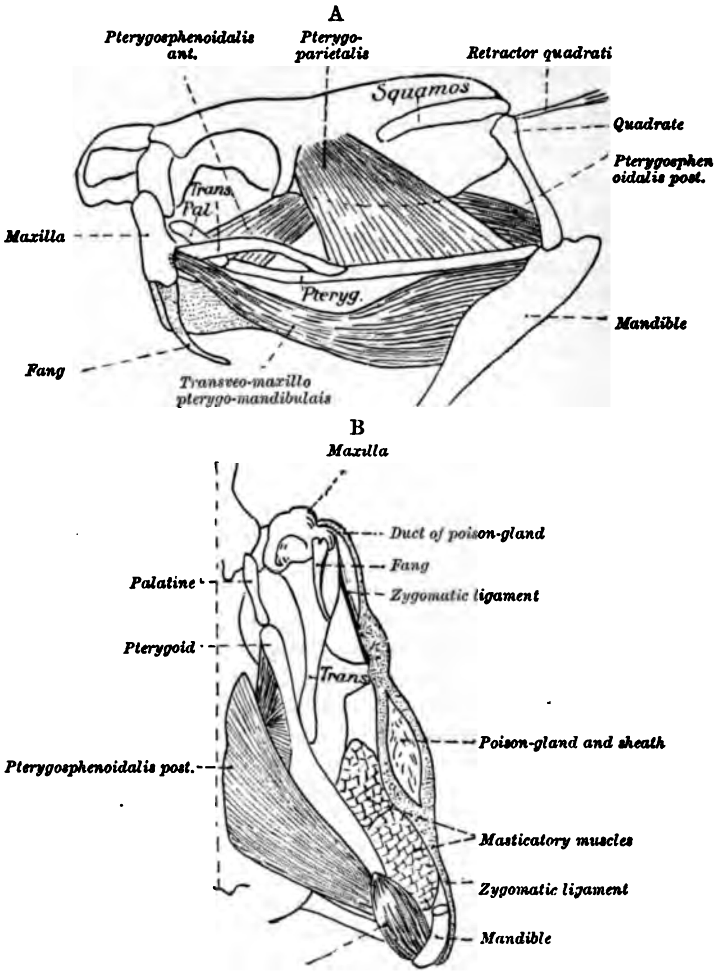

FIG. 238.—HEAD OF THE VIPER (after Katheriner).

A, from the left side: the integument, zygomatic ligament, poison-gland, jaw-muscles, and palatine and pterygoid teeth are not indicated. B, left side from below: the muscles of the jaw are cut through transversely, and part of the sheath of the poison-gland is slit open.

Birds.—In Birds, and more especially in climbing Birds (Scansores), a well-developed lingual gland is present opening on the floor of the mouth, and another at the angle of the latter.

There is no doubt that the lingual glands are to a great extent homologous with those of Lizards, but it is not known whether the gland at the angle of the mouth corresponds with the posterior upper labial gland of Reptiles—that is, to the poison-gland of Snakes. The median palatine glands of Birds are not homologous with those of Reptiles, and labial glands are wanting. The lingual glands are supplied by the glossopharyngeal, the others by the trigeminal.

Mammals.—Three larger sets of salivary glands which have become secondarily separated from one another may be distinguished in connection with the mouth in Mammals: these are called, according to their position, (1) *parotid*, (2) *submaxillary*, and (3) *sublingual*. Each of the two former opens into the mouth by a well-defined duct, that of the sublingual having several independent ducts. A special *retrolingual* portion usually becomes differentiated from the sublingual gland and communicates with the submaxillary duct. They all have a tubular or tubulo-alveolar structure.[1]

The parotid is usually situated at the base of the external ear. The submaxillary is a compound mucous and serous gland, consisting of elements which differ from one another histologically: it lies beneath the mylohyoid muscle, close to which the retrolingual gland is also situated: the latter is wanting in only a few Mammals (*e.g.* Rabbit, Horse). The sublingual gland extends between the tongue and the alveoli of the teeth, and is rarely absent (*e.g.* Mouse, Mole, Shrew).

With the exception of the parotid, the homology of which is not clear, all these glands, together with certain smaller and less important ones (*buccal, lingual, palatine*, and *labial glands*), are comparable to the oral glands of lower Vertebrates.[2]

Tongue.[3]

Fishes.—The tongue is, rudimentary in Fishes, and, as a rule, is simply represented by a fold of mucous membrane covering the basi-hyoid, which in all the higher Vertebrates serves as a point of origin for many of the lingual muscles. Except in Cyclostomes, where it has to do with the suctorial or boring apparatus, the tongue of Fishes is not capable of movement apart from the visceral skeleton, and is wanting in a proper musculature. It is provided with papillæ and serves only as a tactile organ, or, when provided with teeth (*e.g.* certain Teleosts, Fig. 69), as a prehensile organ also. In Dipnoans the tongue is not more highly differentiated than in many other Fishes.

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[1] In some Mammals (*e.g.* Lepus) there is also an *infraorbital* or *zygomatic salivary gland*, covered by the zygoma and extending into the orbit, its duct opening anteriorly to that of the parotid. Salivary glands are wanting in the Cetacea.

[2] The mucous glands are phylogenetically older than the serous glands, and their essential function is merely to moisten the food. The serous glands have to a greater or less extent become differentiated into an apparatus for producing a secretion containing enzymes and acting chemically on the food.

[3] For the papillæ of the tongue, cf. p. 254.

Amphibians.—In Perennibranchiata and young larvæ of Myctodera the tongue is very similar to that of Fishes, and is comparable only to a small posterior and median part of the definitive tongue of the latter group: the larger, anterior, glandular part is a new formation, and is not represented in Fishes.

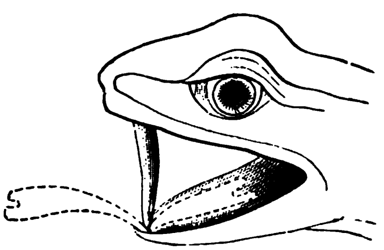

FIG. 239.—FIGURE SHOWING THE TONGUE OF THE FROG IN THREE DIFFERENT POSITIONS.

The definitive tongue is very similar in many Urodeles and Anurans, although various differences are seen in its mode of development in the two groups. Thus in Anura the primitive tongue persists for a much shorter time, and is connected on the floor of the mouth with the more anterior, larger, secondary part in a different way; the muscles are earlier developed and more numerous, and the glands appear very late. In general the tongue is more highly differentiated in Anurans than in Urodeles in consequence of functional adaptation connected with catching the prey.[1]

The surface of the tongue is velvet-like, owing to the numerous papillæ, and its mobility varies greatly in the different forms. It is usually attached only by the anterior end (Fig. 239) or by a portion of its ventral surface: in other cases it is free all round, and in Spelerpes (Fig. 240) is capable of being extended far out of the mouth by means of a complicated mechanism.

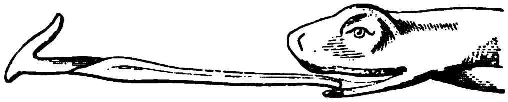

FIG. 240.—HEAD OF *Spelerpes fuscus*, WITH THE TONGUE EXTENDED.

Reptiles.—The tongue of Reptiles reaches a much higher stage of development than that of Amphibians. As in them, its

[1] The rapid movements of the Frog's tongue are effected by the genioglossus and hyoglossus muscles, the former acting as a protractor and the latter as a retractor, while the intrinsic muscles are responsible for gripping the prey. In the Aglossa (Pipa and Xenopus) the tongue has undergone degeneration.

main part arises anteriorly to the primitive larval tongue from an originally independent region lying between the lower jaw and basihyoid, and known in the Amniota as the *tuberculum impar.* To this, however, are added portions belonging to the region of the median part of the hyoid and part of the first branchial arch, as well as extensive lateral ridges belonging to the mandibular region, and this fact accounts for the presence of an additional lingual nerve—a branch of the third division of the trigeminal—which is wanting in Amphibians. The tongue is provided with numerous sensory organs, but no glands are present within it. It is usually very mobile (least so in Chelonians and Crocodiles), and part of it may be enclosed by a "sheath" (Fig. 241). In form and relative size it is much more variable than in Amphibians, and this is especially the case in Lizards, in which the tongue is used for classificatory purposes (*Vermilinguia, Crassilinguia, Brevilinguia, Fissilinguia*): in the Fissilinguia and in Snakes it is forked at the apex. In the Chameleon it is protrusible, as in Spelerpes amongst Amphibians, but the mechanism is different in the two cases.

Birds.—Although the early development of the base of the tongue-rudiment in connection with the hyoid and first branchial arch is apparently similar in all Birds and resembles that seen in Reptiles, many differences are noticeable in its subsequent development in the various groups of Birds (*e.g.* Lamellirostres and Fringillidæ), and these concern the tuberculum impar and the modification of its anterior region in connection with various functional adaptations. Important differences are seen in the muscles and nerves as compared with Reptiles. A sensory branch of the trigeminal nerve is wanting, and is replaced functionally by the strongly developed glossopharyngeal.

The tongue of Birds is in general poorly provided with muscles. It usually possesses a horny covering and is provided with papillæ and pointed, recurved processes; it may, as in many Reptiles, be split up at its distal end, being either bifurcated (Trochilidæ) or having a brush-like form. In Woodpeckers (cf. p. 123) the tongue may be thrown far out from the mouth by means of a complicated system of muscles, and it thus serves as a prehensile organ. The tongue is relatively largest in predatory Birds (Rapaces) and Parrots: in the latter it is soft and cushion-like, its size being due not so much to the special development of muscles as to the presence of fat, vessels, and glands.

Mammals.—The tongue reaches its most complete morphological and physiological development in Mammals, and undergoes the most various modifications in form and function. It is as a rule flat, band-like, and rounded anteriorly, is rich in glands[1] and

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[1] A gland on the apex of the tongue (gland of Blandin or Nuhn) occurs in Man, the Orang-outan, and Sheep.

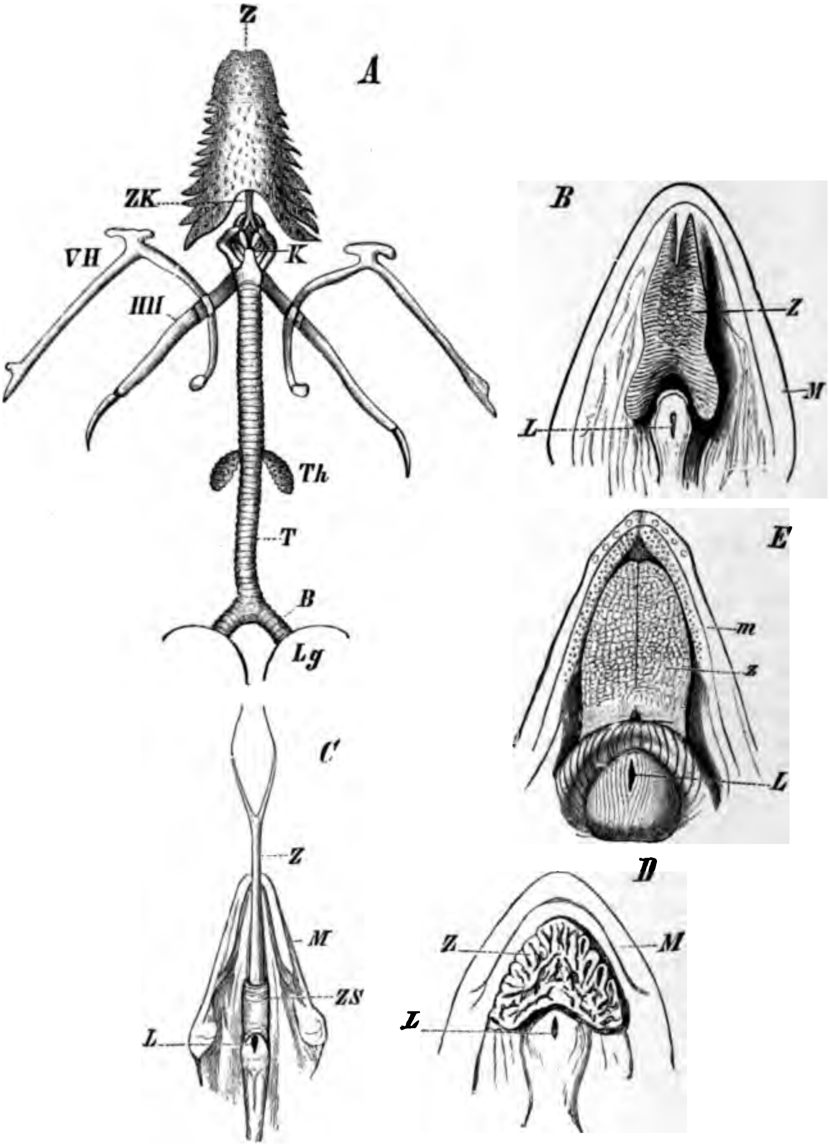

Fig. 241.—A, Tongue, Hyoid-Apparatus, and Bronchi of a Gecko (*Phyllodactylus europæus*); B, Tongue of *Lacerta*; C, of *Monitor indicus*; D, of *Emys europæa*; E, of an Alligator.

B, bronchi; *HH* and *VII*, anterior and posterior cornua of hyoid-apparatus; *K*, larynx; *L*, glottis; *Lg*, lung; *M*, mandible; *T*, trachea; *Th*, thyroid; *Z*, tongue; *ZK*, entoglossal bone; *ZS*, sheath of tongue.

is always extensile except in the Cetacea. The intrinsic musculature is highly developed, and may even extend backwards over the sternum (Manis, Myrmecophaga). In the Ruminants, in which upper incisors are wanting, it is very important in browsing. In some cases (*e.g.* Felidæ) its surface is horny.[1] A fold, the so-called *sublingua* (plica fimbriata), is present on the lower surface of the tongue, and is especially well marked in Lemurs; in the Slender Loris (Stenops) it is supported by cartilage.[2] This structure has been supposed to correspond to the last vestige of the tongue of lower Vertebrates (Reptiles) which has been replaced by the more highly-developed organ characteristic of Mammals, the latter having arisen secondarily from the reduced sublingua.[3]

THYROID.

In Amphioxus, as in Ascidians (Tunicata), a ciliated groove, the *endostyle*, is present along the ventral border of the extensive pharynx, and the cells lining this groove secrete a glutinous substance in which the food particles become entangled and by the action of the cilia are carried onwards to the intestine. This endostyle is without doubt homologous with the *thyroid* of Craniates, the presence of which is as characteristic of them as is the notochord. In consequence, however, of the different method of taking in food and the presence of jaws, it has undergone a change of function and never remains open to the pharynx throughout life, but gives rise to a so-called "ductless gland," the substance formed by its "internal secretion" passing into the lymph or blood.

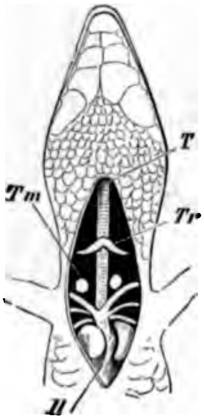

FIG. 242.—THYROID AND THYMUS OF *Lacerta agilis*.

H, heart; *T*, trachea; *Tm*, thymus; *Tr*, thyroid.

The thyroid arises primarily as a median ventral diverticulum of the pharynx which extends along the region of the first four or five visceral clefts, and in the course of development may become subdivided into two lobes. In addition to this unpaired diverticulum, paired portions, situated more posteriorly, are developed in Mammals: the former, as in all Gnathostomes, arise from the basihyal region,

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[1] Horny papilla are present on the tongue of Ornithorhynchus.

[2] The so-called "*lyssa*" of the Mammalian tongue consists partly of cartilage, and partly of muscle, fat, and connective tissue: it corresponds to a vestige of the lingual cartilage of lower Vertebrates, and undergoes various modifications.

[3] According to another view, the sublingua is not a vestige, but a structure appearing for the first time in certain Mammals which has been secondarily differentiated from a ventral portion of the tongue proper: even then, however, its cartilage may have an ancestral significance.

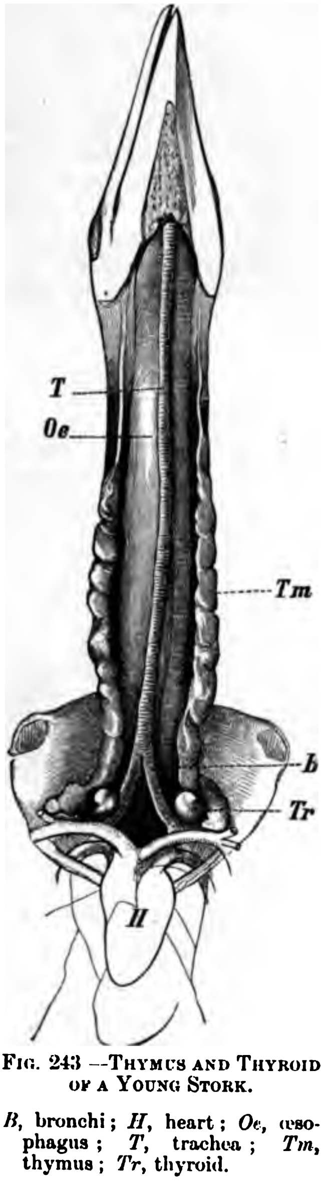

FIG. 243 —THYMUS AND THYROID OF A YOUNG STORK.

B, bronchi; *H*, heart; *Oe*, œsophagus; *T*, trachea; *Tm*, thymus; *Tr*, thyroid.

just in front of which is the tuberculum impar of the tongue-rudiment.

In the Ammocœte, the simple diverticulum, which is lined by ciliated epithelium, opens into the pharynx between the third and fourth clefts (Fig. 260), but in the adult Petromyzon the organ, as in all Craniata, loses its connection with the pharynx and undergoes considerable reduction and a change of function, giving rise to numerous closed follicular masses.[1]

In Elasmobranchs the thyroid is unpaired and lies behind the mandibular symphysis, just in front of the bifurcation of the ventral aorta; in adult Teleosts it is paired, and is situated in the region of the first branchial arch. In Dipnoans it lies anteriorly to the muscles of the visceral skeleton and shows an indication of a division into right and left lobes.

In the Urodela and Anura the thyroid is situated close to the anterior end of the pericardium: it undergoes subdivision and forms numerous vesicles lying posteriorly to the second ceratobranchials in the former, and on the ventral side of the posterior cornua of the hyoid in the latter.

In Lizards the thyroid is situated close to the trachea, slightly behind the middle of its course (Fig. 242), and in Chelonians and Crocodiles it usually possesses right and left lobes lying on the great vessels just after they leave the heart. In Birds (Fig. 243) the organ is paired, and has a similar position.

The thyroid of Mammals (Fig. 227) consists of two lobes often connected by a median isthmus situated on the ventral side of the larynx and trachea, and if well developed, constituting a " middle lobe."[1]

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[1] In Myxine the thyroid consists of rounded or oval capsules surrounded by fat; they are nearly all median and are arranged separately or in groups between the gill-sacs on either side, the gullet above, and the ventral aorta below.

The function of the thyroid is not thoroughly understood, but the organ is essential for the well-being of the individual, its extirpation commonly resulting in various disturbances of the mental and organic functions. It is extremely vascular, especially in Mammals, and gives rise to a substance which may contain iodine.

THYMUS.

The thymus has always a paired, epithelial origin, and is thus primarily of a glandular nature: its epithelial character is retained throughout life, although the large cells of which it is orginally composed undergo a marked subdivision into smaller elements.

In Cyclostomes, the presence of a thymus has not been proved. In Elasmobranchs it arises on either side from the endodermic epithelium lining the upper angles of the first five gill-clefts, near the ganglia of the ninth and tenth cerebral nerves, as well as in the neighbourhood of the spiracle: it appears that all the gill-pouches originally took part in its formation, as is also indicated in Teleosts, Cæcilians, and even in Snakes.

In Teleostomes and Dipnoans, the thymus is similarly situated dorsally to the branchial region, but certain modifications occur, part of it undergoing resorption, while a subdivision into lobes or a secondary fusion of originally distinct parts occurs. In adult Urodeles and Anurans it lies behind and above the articulation of the lower jaw.

In all the Amniota, the thymus is developed in connection with the three or four anterior pharyngeal pouches. In adult Snakes, and also in Lizards and Chelonians, it consists of two or more separate lobes situated near the carotid arteries. Young Crocodiles and Birds possess an elongated, band-like, lobed thymus extending along the neck (Fig. 243).[2] In Mammals usually only a small portion of the organ is present in the cervical region, its greater part being situated in the thorax, just above the sternum. In young animals it is usually very voluminous, and increases in size up to sexual maturity, then gradually becoming reduced, without however, losing its function, whatever that

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[1] Under the term *parathyroids*, or "accessory thyroids," are understood those parts of the thyroid which may arise from its unpaired rudiment (*ductus thyreoglossus*). The so-called "epithelial bodies" formed from the second to the fifth pharyngeal pouches, as well as the *ultimobranchial* (*postbranchial*) body arising from the most posterior cleft, have nothing to do with the thyroid, although they may come into intimate relation with it as well as with the thymus. The structure known as the "*carotid gland*" in Mammals, which is situated at the bifurcation of the common carotid artery of either side, belongs to a peculiar category of organs which have genetic relations to the sympathetic system (cf. p. 247): a similar structure is said to be present in Birds.

[2] Muscular elements occur in the thymus of Amphibia and Sauropsida.

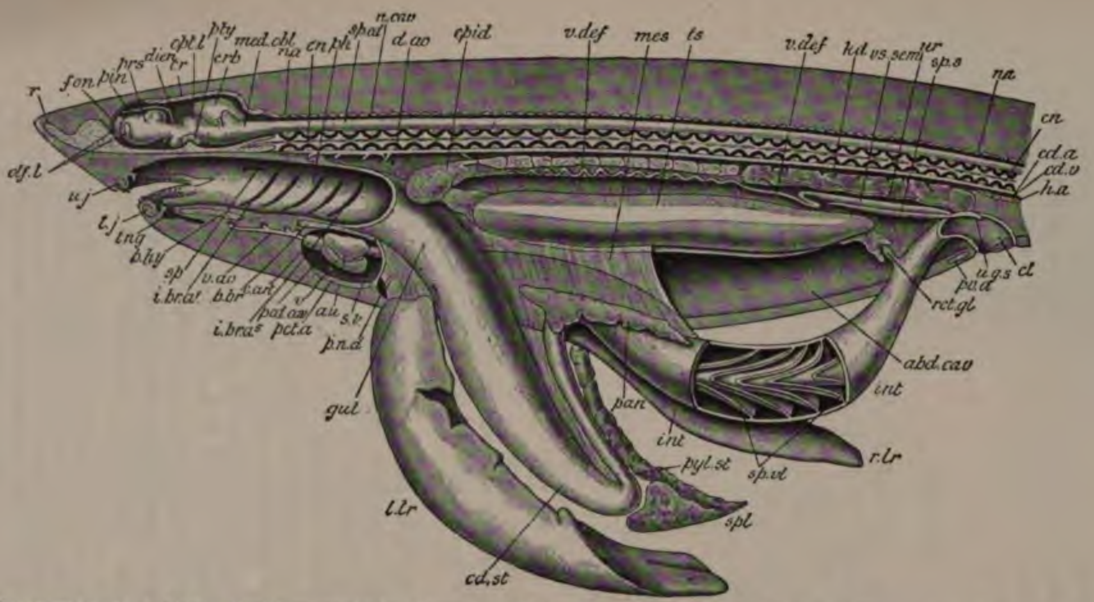

FIG. 244.—DISSECTION OF A MALE *Scyllium canicula*, from the left side. (From T. J. Parker's *Elementary Biology.*) The left side of the body-wall is cut away to the median plane so as to expose the abdominal (*abd. cav.*), pericardial (*pcd. cav*), and neural (*n. cav*) cavities in their whole length.

In the skeleton the cartilaginous parts are dotted, and the calcified ends of the centra (*cn*) black. *n.a*, neural arches; *h.a*, hæmal arches; *cr*, cranium; *r*, rostrum; *u.j*, upper jaw; *l.j*, lower jaw; *b.hy*, basihyal supporting tongue (*tng*); *b.br*, basibranchial; *pct.a*, pectoral arch; *pv.a*, pelvic arch; *fon*, fontanelle.

The alimentary canal with the liver (*l.lr*, *r.lr*), &c., has been displaced downwards, and the oral cavity and pharynx (*ph*), part of the intestine (*int*), and the cloaca (*cl*) have been opened. *sp*, spiracle; $i.br.a^1$—$i.br.a^5$, internal branchial apertures; *cd.st*, cardiac, and *pyl.st*, pyloric portions of stomach; *sp.vl*, spiral valve of intestine (*int*); *pan*, pancreas; *spl*, spleen; *rct.gl*, rectal gland; *mes*, mesentery.

s.v, sinus venosus; *au*, auricle; *v*, ventricle; *c.art*, conus arteriosus; *v.ao*, ventral aorta with origins of the afferent branchial arteries; *d.ao*, dorsal aorta, receiving the efferent branchial arteries anteriorly, and posteriorly becoming the caudal artery (*cd.a*) lying above the caudal vein (*cd.v*).

sp.c, spinal cord; *med.obl*, medulla oblongata; *crb*, cerebellum; *opt.l*, optic lobes; *dien*, diencephalon; *prs*, telencephalon; *olf.l*, olfactory lobes; *pin*, pineal body; and *pty*, pituitary body.

kd, left kidney; *ur*, duct of kidney; *u.g.s*, urinogenital sinus; *ts*, left testis; *epid*, epididymis; *v.def*, vas deferens; *vs.sem*, vesicula seminalis; *sp.s*, sperm-sac; *p.n.d*, vestige of Müllerian duct.

function may be: at any rate it is not a "lymphoid organ," and the origin of the leucocytes occurring in it is not known.[1]

ŒSOPHAGUS, STOMACH, AND INTESTINE.

Ichthyopsida.—The œsophagus in the Anamnia is short, and usually not distinctly marked off from the stomach, though exceptions to this rule often occur (*e.g.* many Teleostei, Siren lacertina).

The stomach is often defined as a widened section of the enteric canal situated between the posterior end of the gullet and the entrance of the bile duct. Such a dilatation can strictly only be spoken of as a stomach when its epithelium possesses specific characteristics and gives rise to *gastric glands*: in this sense a stomach is wanting in Amphioxus, Cyclostomi, Holocephali, certain Teleostei (*e.g.* Cyprinidæ, certain Labridæ, Gobiidæ, and Bleniidæ, Syngnathus, Cobitis), and Dipnoi (Fig. 247). In many Teleosts the bile-duct opens far forwards, so that the gastric region is very short.

In other Fishes, as well as in all Amphibians, a true stomach is present, and is usually externally recognisable as a more or less dilated sac; it may be curved on itself, so as to form a U-shaped loop, the two (cardiac and pyloric) limbs of which lie parallel to one another (Fig. 244). In general, its form is adapted to that of the body: thus Rays and Anurans possess a far wider stomach than do most other Fishes and Amphibians (cf. Figs. 244–249). The stomach of Teleosts varies considerably in form.[2]

The intestine may be straight or nearly straight, or may be more or less coiled, and in the former case a *spiral fold* or *valve* may be developed in Fishes, to increase the absorptive surface.

In the Lamprey a longitudinal fold or *typhlosole*, taking a slightly spiral course, extends into the lumen of the intestine. In Elasmobranchs, Ganoids, and Dipnoans, the fold is more highly developed and forms a well-marked spiral valve, the turns of which may lie so close together as to almost fill the cavity of the intestine (Fig. 244).[3] In the Ganoids it begins to undergo degeneration: thus in Lepidosteus it is only present in the hinder part of the intestine (Fig. 245). Traces of a spiral valve can even be recognised amongst the Teleostei (Cheirocentrus).

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[1] The so-called "Hassal's corpuscles" in the thymus arise secondarily from groups of the small epithelial cells.

[2] In numerous Teleosts (*e.g.* Tinca vulgaris, Cobitis fossilis) outer longitudinal and inner circular *striated* fibres are present in both stomach and intestine externally to the unstriated muscular coat. They grow backwards from the œsophagus.

[3] The arrangement and extent of the valve vary considerably; it may begin close behind the pylorus, or the valveless anterior part ("bursa entiana") may be relatively longer. In some cases the valve is scroll-like, and not spiral (*e.g.* Carcharias).

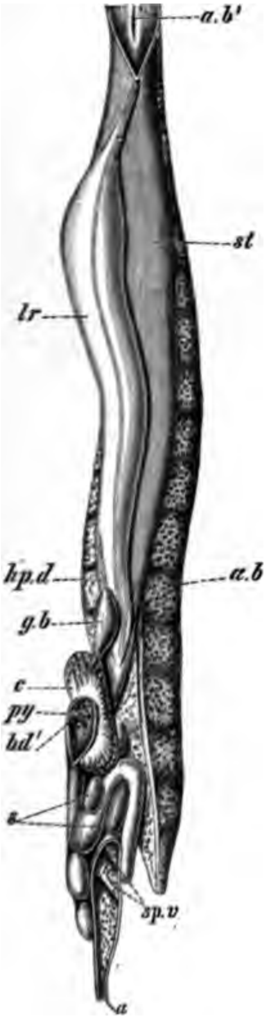

FIG. 245.—ALIMENTARY VISCERA AND SWIM-BLADDER OF *Lepidosteus* (*in situ*). (After Balfour and Parker.)

a, anus; *a.b.* swim-bladder; *a.b*¹, its aperture into the throat; *b.d*¹, aperture of bile-duct into intestine; *c*, pyloric cæca; *g.b*, gall-bladder; *hp.d*, hepatic duct; *lr*, liver; *py*, pyloric valve; *s*, spleen; *sp.v*, spiral valve; *st*, stomach.

Pyloric cæca are met with in Ganoids (except Amia) and most Teleosts, and consist of longer or shorter finger-shaped processes of the small intestine, situated posteriorly to the pylorus in the region of. the bile-duct (Figs. 245, 246). Their number varies from 1 (Polypterus and Ammodytes) to 191 (Scomber scomber): in some fishes they are bound together by connective tissue so as to form a compact mass. The Shark Læmargus possesses a pair of cæca opening into the anterior part of the intestine.

In the narrow-bodied Gymnophiona the intestine is only slightly coiled, while in Anura it becomes considerably folded on itself: its form in Salamanders is about mid-way between these two extremes.

In the Cyclostomi, Holocephali, Ganoidei, and most Teleostei, there is a separate anus; in all other Fishes as well as in the Amphibia the large intestine opens into a *cloaca*, common to it and to the urinogenital ducts. The large intestine (rectum) is comparatively short and takes a straight course; in Amphibians, as well as to some extent in certain Ganoids and Teleosts, it is plainly marked off from the small intestine by its size, and between the two there is often a circular valve. In some cases the rectum is considerably swollen and may even exceed the stomach in capacity (Fig. 249). An outgrowth of the ventral wall of the cloaca in Amphibia gives rise to the *urinary bladder* and represents the *allantois* (*q.v.*) of higher forms.

In Plagiostomes a finger-shaped *rectal gland* (*processus digitiformis*)[1] opens into the anterior part of the rectum, and this perhaps corresponds to the blind gut or *cæcum* of higher forms. Traces of a cæcum are seen in certain Teleosts (*e.g.* Box). In the

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[1] In the Holocephali there is no processus digitiformis, but the thick wall of the rectum encloses numerous gland-tubules.

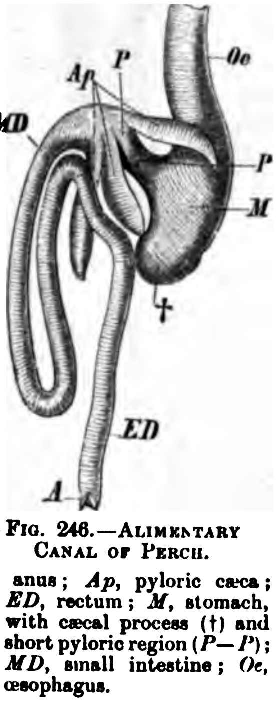

FIG. 246.—ALIMENTARY CANAL OF PERCH.

A, anus; *Ap*, pyloric cæca; *ED*, rectum; *M*, stomach, with cæcal process (†) and short pyloric region (*P*—*P*); *MD*, small intestine; *Oe*, œsophagus.

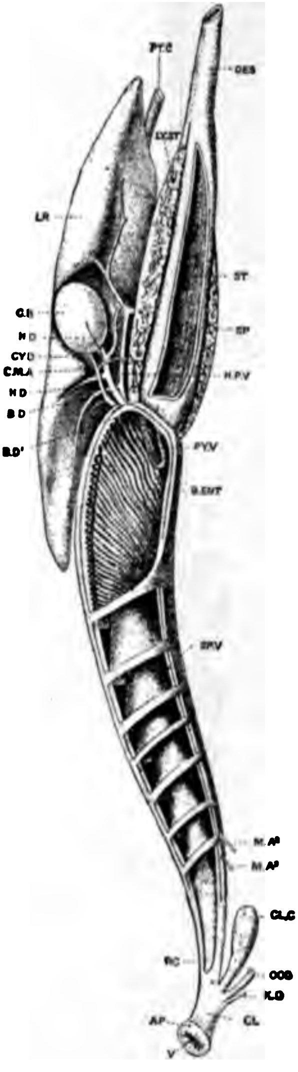

FIG. 247.

FIG. 247.—ALIMENTARY CANAL AND APPENDAGES OF *Protopterus annectens*. (After W. N. Parker.)

ap, abdominal pore; *b.d*, common bile duct, and *b.d*¹, its aperture into the intestine; *b.ent*, bursa entiana (anterior portion of intestine); *cl*, cloaca; *cl.c*, cloacal cæcum; *c.m.a*, cœliaco-mesenteric artery; *cy.d*, cystic duct, *g.b*, gall-bladder; *h.d*, hepatic ducts; *h.p.v*, hepatic portal vein; *k.d*, base of kidney duct; *lr*, liver; *m.a*², *m a*³, mesenteric arteries; *ood*, base of oviduct; *oes*, œsophagus; *py.v*, pyloric valve; *rc*, rectum; *sp*, spleen; *sp.v*, spiral valve; *st*, "stomach"; *v*, vent. The pancreas is not seen, as it is embedded in the walls of the stomach and anterior part of the intestine on the dorsal and right side.

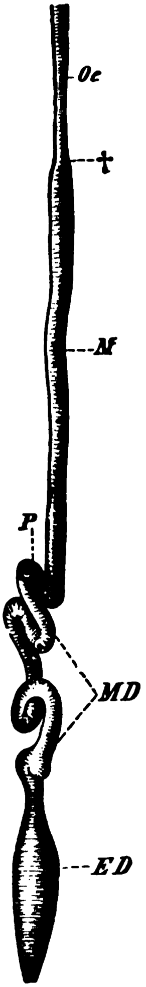

FIG. 248.

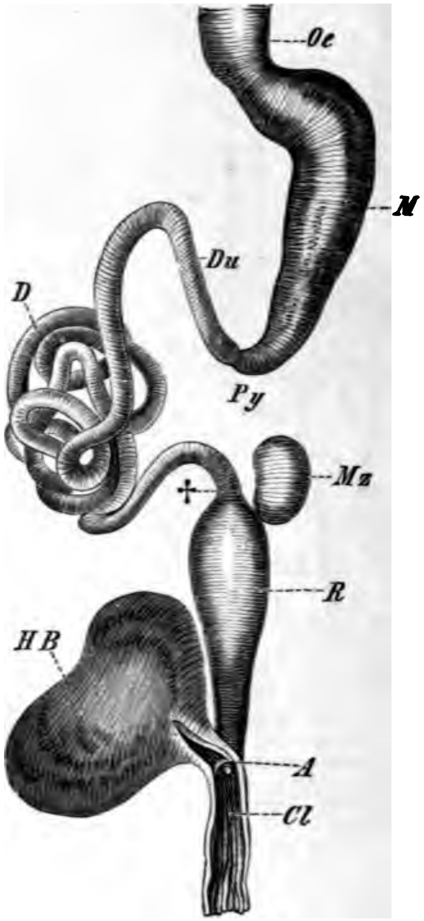

FIG. 249.

FIG. 248.—ALIMENTARY CANAL OF *Siren lacertina*.

ED, large intestine; *MD*, small intestine; *Oe*, œsophagus, marked off from the stomach (*M*) by a constriction (†); *P*, pyloric region.

FIG. 249.—ALIMENTARY CANAL OF *Rana esculenta*.

A, opening of the rectum into the cloaca (*Cl*); *D*, ileum; *Du*, duodenum; †, boundary between small and large intestine; *HB*, urinary bladder; *Oe*, œsophagus; *M*, stomach; *Mz*, spleen; *Py*, pyloric region; *R*, rectum.

Dipnoi a cloacal cæcum is present (Fig. 247; cf. under Urinogenital Organs).

In all Fishes in which a cloaca is wanting, the anus is anterior to the urinogenital aperture.

Reptiles.—In correspondence with the more definitely differentiated neck, the œsophagus of Reptiles is relatively longer than in the animals as yet considered; it is always plainly marked off from the much wider stomach, which is usually sac-like, or bent upon itself, in which latter case it lies transversely (Chelonians).[1] As regards external form, the stomach of Crocodiles is more specialised than that of other Reptiles, approaching that of Birds.

Snakes, snake-like Lizards, and Amphisbænians possess a narrow, spindle-shaped stomach, which lies in the long axis of the body; in correspondence with the large size of the masses of food, which are swallowed whole, it is capable of great distension. In these the intestine is only slightly coiled: in other Lizards the coils are more marked, and in forms with broad bodies (*e.g.* Chelonians, Crocodiles) the folding is carried still further.

The large intestine has a straight course, is often considerably swollen, and opens into a cloaca. It may (*e.g.* certain Chelonians) be as long as the small intestine and be bent on itself. [For the urinary (allantoic) bladder present in many Reptiles, cf. under Fœtal Membranes and Urinary Organs.]

In many Reptiles (*e.g.* most Lizards, Snakes), a small blind-gut or cæcum is present at the anterior portion of the large intestine: it is generally asymmetrical.

Birds.—In correspondence with the kind of nutriment, the mode of life, and the absence of teeth, certain modifications of the œsophagus and stomach occur in Birds. In graminivorous Birds and Birds of Prey either the whole gullet forms a dilated sac or else it gives rise to a ventral outgrowth; in both cases the enlargement is known as the *crop* (*ingluvies*) (Fig. 250, A). This serves as a food reservoir, and in some cases its walls are glandular.

The stomach, instead of remaining simple, generally becomes divided externally into two portions, an anterior and a posterior. The former, which on account of its richness in glands is called the glandular stomach (*proventriculus*), alone takes part in dissolving the food; while the latter, which is lined by a keratinoid layer consisting of a hardened glandular secretion, has simply the mechanical function of grinding the food, in correlation with which a very peculiar and thick muscular wall provided with two tendinous discs is developed (Fig. 250, B and C). The degree of development of this muscular stomach, or *gizzard*, is in direct proportion to the consistency of the food. Graminivorous Birds possess the strongest muscular layer and the thickest keratinoid lining, while in the series of insectivorous Birds, up to the Birds of Prey, this condition becomes gradually less marked, and the division of labour is not so noticeable. Thus in the series of existing Birds we can trace the course of the phylogenetic differentiation of the organ.

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[1] The œsophagus of marine Chelonians, like that of many Birds, is lined by horny papillæ, and in the stomach a differentiation of distinct gland-zones is seen, such as is already indicated in certain Fishes and is carried still further in Mammals.

The small intestine is usually of considerable length and becomes folded on itself to a greater or less degree ; it varies, however, in form, relative length, and diameter.

The straight large intestine opens into a cloaca, and differs as to its relative diameter. The cæcum is usually paired, and may be extremely long (Lamellirostres, Rasores, Ratitæ). All kinds of intermediate stages between this condition and an entire absence of a cæcum are to be met with. When largely developed, it must have an important relation to digestion, as an increase of surface of the mucous membrane is thus effected ; this increase may even be carried further by each cæcum being provided with a spiral fold consisting of numerous turns, as in the Ostrich.

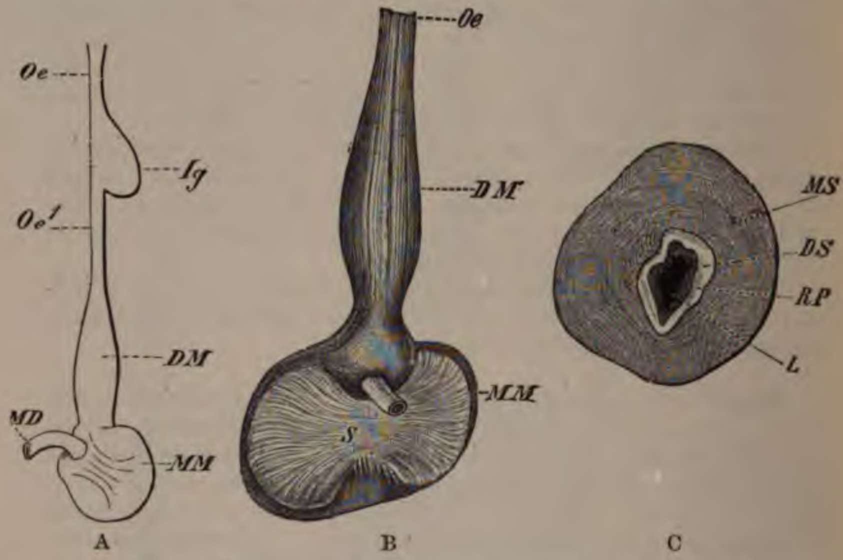

FIG. 250, A.—DIAGRAM OF THE ŒSOPHAGUS AND STOMACH OF A BIRD. *DM*, glandular stomach ; *Ig*, crop ; *MD*, duodenum ; *MM*, muscular stomach ; *Oe*, *Oe*¹, œsophagus.

FIG. 250, B.—GLANDULAR STOMACH AND GIZZARD OF *Fulica atra*. *S*, tendrinous disc. (Other letters as in A.)

FIG. 250, C.—TRANSVERSE SECTION THROUGH THE LATERAL PART OF THE GIZZARD OF *Tetrao urogallus*. *DS*, glandular layer ; *L*, lumen ; *MS*, muscular layer ; *RP*, keratinoid triturating layer.

This so-called *bursa Fabricii* is a structure peculiar to Birds, and arises as a small, solid, epithelial outgrowth from the ectodermal portion of the cloaca (proctodæum), later becoming excavated to form a vesicle. It is situated in the pelvic cavity between the vertebral column and the posterior portion of the intestine, opening into the outer section of the cloaca posteriorly to the urinogenital ducts. It is probably present in all Birds, but becomes atrophied more or less completely in the adult; its physiological function is unknown.

Mammals.—The œsophagus, like that of Birds, is sharply marked off from the stomach, and its muscles consist for a greater or less extent of striated fibres derived from those of the pharynx.

The stomach undergoes much more numerous modifications than are met with in any other vertebrate Class. As a rule it takes a more or less transverse position and has a sac-life form, the *cardiac* portion, into which the œsophagus opens, and the *fundus*, which lies towards the left side of the abdomen being usually more swollen and having thinner walls than the *pyloric* portion, which communicates with the duodenum. The gastric glands have in general a different histological and physiological character in the three regions of the stomach, so that three glandular zones may be distinguished (Fig. 251, and cf. p. 345)

According to the definition given on p. 335, a true stomach is wanting in Monotremes (Fig. 251, A); and although the organ is represented by a wide sac, it is entirely wanting in glands, and is lined throughout by stratified epithelium: this condition is doubtless secondary. Amongst Edentates, a similar peculiarity is seen in Manis javanica—in which, however, some of the glands are retained in a sac-like outgrowth from the greater curvature, the rest of the stomach being lined by a horn-like layer.

In herbivorous Mammals the stomach is, as a rule, relatively larger and more complicated than in carnivorous Mammals, and it may become divided into two or more chambers. In Bradypus, many Rodents (Muridæ) and in the Horse distinct cardiac and pyloric chambers can be recognised, and in herbivorous Marsupials and Ungulates numerous intermediate forms between a simple and an exceedingly complex stomach, such as occurs in the typical Ruminants, are to be met with (Fig. 251). In the latter (Fig. 252) the stomach is divided into four chambers, which are called respectively *rumen* (paunch), *reticulum*, *psalterium*, and *abomasum*. The two first, which may be looked upon as parts of one and the same chamber, simply serve as storage cavities, the food returning from them into the mouth, once more to undergo mastication. It then again passes down the gullet, and is conducted along a groove to the psalterium, the edge of the groove closing, and finally into the abomasum, the latter alone being provided with peptic (rennet) and pyloric glands, and serving as the true digestive stomach: the other chambers are almost or entirely glandless, and are lined by pavement epithelium.

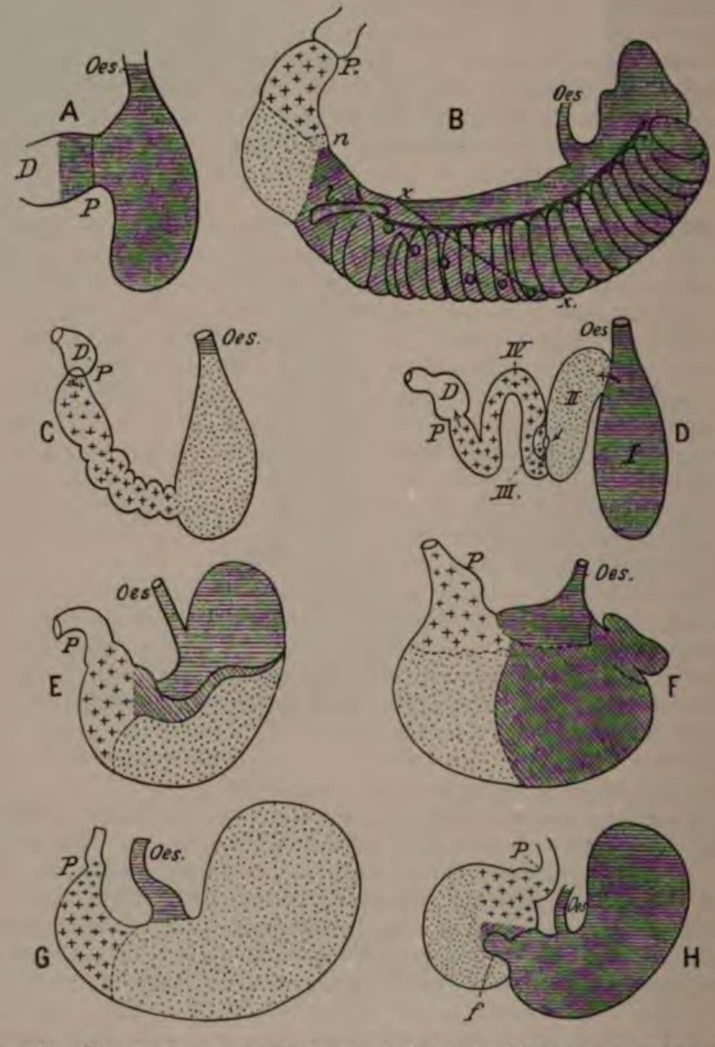

FIG. 251.—DIAGRAMS OF THE STOMACH IN VARIOUS MAMMALS SHOWING THE DIFFERENT REGIONS. (After Oppel.)

A, ORNITHORHYNCHUS; B, KANGAROO (*Dorcopsis luctosa*); C, TOOTHED WHALE (*Ziphius*); D, PORPOISE; E, HORSE, F, PIG; G, HARE; H, HAMSTER (*Cricetus frumentarius*).

The œsophageal region (lined by stratified epithelium) is indicated by transverse lines; the region of the cardiac glands by oblique lines; that of the fundus-glands by dots; and that of the pyloric glands by crosses.

D, duodenum; *f* (in H), fold bounding the œsophageal region; *I—IV* (in D), the four chambers of the stomach; *l* (in B), lymphoid tissue; *Oes*, œsophagus; *P*, pylorus; *x...x* (in B), boundary line between the œsophageal and cardiac regions.

The psalterium is the latest to be differentiated both phylogenetically and ontogenetically, and is rudimentary in the Tragulidæ. In Camels the rumen gives rise to two masses of gland-containing outgrowths, known as "water-cells": the latter are separated from one another by septa and provided with sphincter-like muscles. In the Cetacea (Fig. 251, C and D) and Hippopotamus, the stomach is divided into several chambers, and various other modifications in form and structure are met with amongst Mammals. Thus in the Kangaroo, for instance (Fig. 251, B), the walls of the stomach are curiously folded, and in the blood-sucking Bat, Desmodus, the pyloric region gives rise to a cæcum two-thirds as long as the whole intestine.

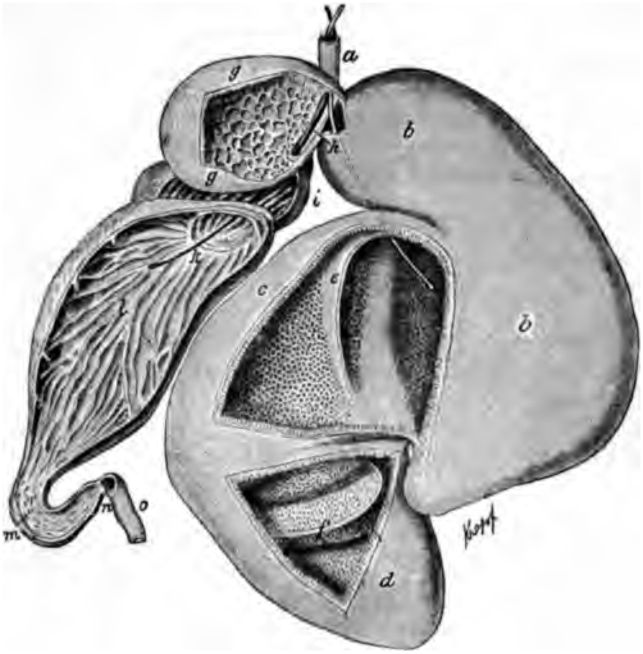

FIG. 252.—STOMACH OF SHEEP. (From Oppel, after Carus and Otto.)
a, œsophagus; *b*, *c*, *d*, the three subdivisions of the rumen, marked off from one another by the folds *e* and *f*; *g*, reticulum; *h*, œsophageal groove; *i*, psalterium; *k*, aperture leading from the psalterium into the abomasum (*l*, *m*); *n*, pyloric valve; *o*, duodenum.

The small intestine is usually long, and varies more as to relative length and diameter in domesticated than in wild forms: its first part, as in Birds, usually forms a duodenal loop.

The large intestine, which is made up of a varying number of coils, usually reaches a great length, and its diameter is much greater than that of the small intestine: these two portions are thus sharply marked off from one another, and the distinction between them is rendered still more marked by the sacculations of the anterior part of the large intestine. Only the posterior portion of the latter, or rectum, which passes into the pelvic cavity, corresponds to the large intestine of lower Vertebrates; the remaining and far larger part occurs only in Mammals, and is called the *colon*.

The cæcum, which is almost always present, undergoes various modifications both as to form and size. Thus in Edendates (Manis, Bradypus), many Carnivora, Odontoceti, Insectivora, and Cheiroptera, it is very small or even entirely wanting, while in Herbivora it may exceed the whole body in length. An inverse development in size is usually noticeable between it and the rest of the large intestine. In many cases (certain Rodents, Anthropoid Apes, and Man) an arrest of a portion of the cæcum takes place in the course of individual development, so that little more than the distal end (*processus vermiformis*) remains (Fig. 227). In Lepus the enormous cæcum is provided with a spiral valve, and in Hyrax, besides a large sacculated cæcum at the junction of the small and large intestines, there is a pair of large, simple, conical cæca further back.

Monotremes only amongst Mammals possess a distinct cloaca, though in Marsupials and some Rodents and Insectivores (especially in the female) the anal and urinogenital apertures are surrounded by a common sphincter. In other Mammals these apertures become completely separated from one another.

HISTOLOGY OF THE MUCOUS MEMBRANE OF THE ALIMENTARY CANAL.

The epithelium lining the alimentary canal of Vertebrates—with the exception of that of the mouth and cloaca, which is usually stratified—consists primitively, that is, phylogenetically, of amœboid or ciliated cells. In some cases this is also true ontogenetically, and in Amphioxus and Protopterus for instance, the ciliated epithelium persists throughout life and in the Lamprey until metamorphosis. In the adult Petromyzon, as well as in many Fishes and even Amphibians, ciliated epithelium occurs constantly only in certain parts of the gut, and in the higner Vertebrates cilia are only seen exceptionally after the embryonic period, so that, as a rule, only ordinary columnar epithelium is present. A striated margin is observable along the free border of the columnar cells, and may be looked upon as a last indication of the earlier ciliated covering: in some lower Vertebrates (*e.g.* Elasmobranchs, Proteus, Salamander larvæ) the individual cells are even capable of an active amœboid movement. In this active participation of the cells in the process of *absorption* an inheritance from primitive Invertebrates can be recognised (*intracellular digestion*); but, at the same time, *extracellular* digestion, in which no external change in the individual cells can be seen, is always the more important in Vertebrates and occurs exclusively in the higher types.

In Amphioxus, Cyclostomi, and Dipnoi, the whole of the alimentary epithelium must be looked upon as secretory, each individual cell acting as an independent gland. In other Fishes and in Amphibians and Reptiles, a higher stage is reached, inasmuch as groups of cells in the stomach give rise to *tubular glands* of a simple nature. A further differentiation of the cells gradually leads to the condition seen in the gastric glands of Mammals, in which three kinds of glands can be distinguished, viz. *cardiac*, *fundus*, and *pyloric* glands, and in the fundus glands, which have the greatest physiological importance, the cells become differentiated into *chief cells* and *parietal cells*.

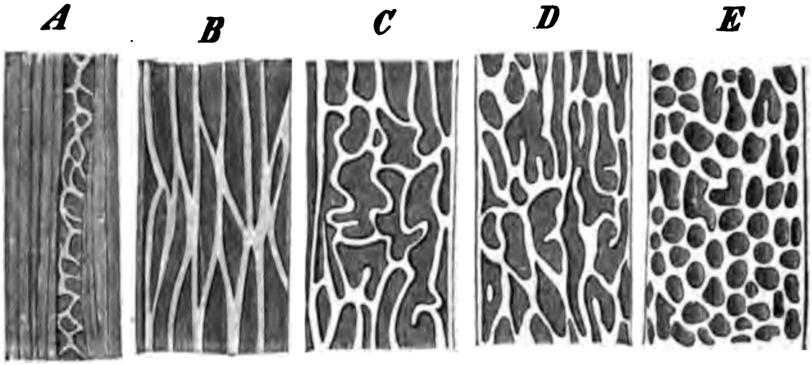

FIG. 253.—SEMIDIAGRAMMATIC FIGURES OF THE MUCOUS MEMBRANE OF THE INTESTINE OF FISHES, SHOWING INTERMEDIATE FORMS BETWEEN LONGITUDINAL FOLDS AND ROUND CRYPTS. (After Edinger.)

A, Petromyzon, showing the spiral fold; *B*, an Elasmobranch; *C* to *E*, various Teleosts.

In the higher Vertebrates, more especially in Birds and Mammals, the epithelium of the intestine also gives rise to tubular *intestinal glands* (*crypts* or *glands of Lieberkühn*) as well as (in Mammals) to Brunner's glands in the duodenum, closely connected phylogenetically with the pyloric glands of the stomach. Mucus-secreting goblet cells are common throughout the alimentary epithelium of Vertebrates, and the same is true of leucocytes: the latter are especially abundant in the submucosa, from whence they may wander into the lumen of the gut. The lymphoid tissue is often aggregated into definite smaller or larger masses or follicles (*e.g. Peyer's patches*), and in some cases (*e.g.* Protopterus) is very abundant.

In order to effect an increase of the absorptive surface, longitudinal folds of the mucous membrane are formed, and a special development of such a fold, taking a spiral course, may result in the formation of a spiral valve. Complications then arise by the development of transverse folds between the longitudinal ones (these are already seen in Elasmobranchs and many other Fishes); and by still further modifications, crypts of varied form and depth are produced, into which open the microscopic glands, when present (cf. Fig. 253). Finger-shaped outgrowths or *villi* of the mucous membrane of the intestine are first plainly distinguishable in Amphibians (especially Anura) and are especially well developed in Mammals.[1]

Appendicular Organs of the Alimentary Canal.

LIVER.

The liver, the form of which is always closely adapted to that of the surrounding parts (Figs. 254 and 255), and which is typically lobed, underlies to a greater or less extent the ventral side of the intestinal tract, and is present in all the Craniata. It arises in the form of a tubular gland,[2] as an outgrowth from the endodermic epithelium of the intestine close to the junction of the

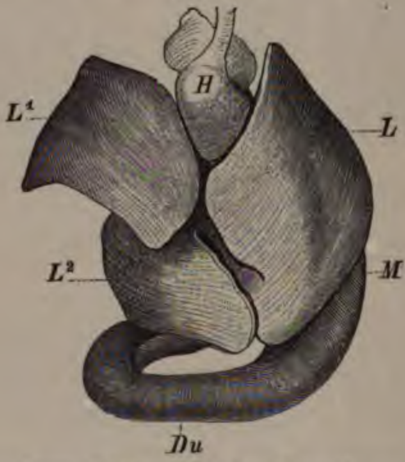

FIG. 254.—LIVER OF *Rana esculenta*. From the ventral side.

Du, duodenum; *H*, heart; *L*, L^1, L^2, the different lobes of the liver; *M*, stomach. A gall-bladder is present, but is not indicated.

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[1] The transverse folds of the mucous membrane occurring *e.g.* in Ratitæ and Mammalia in the small and large intestine are known respectively as *plicæ circulares* (*valvulæ conniventes*) and *plicæ semilunares*.

[2] Further differentiations occur, which gradually lead to a dendritic or net-like arrangement of the gland-ductules, and this shows great variation in different groups and in different stages of development.

latter with the stomach. Both ontogenetically and phylogenetically the liver is an older organ than the pancreas, which is developed from the same endodermal matrix.

In Amphioxus a simple sac-like cæcum (Fig. 258) arises from the intestine just behind the pharynx, and this "hepatic cæcum" may probably be looked upon as the rudiment of a liver.

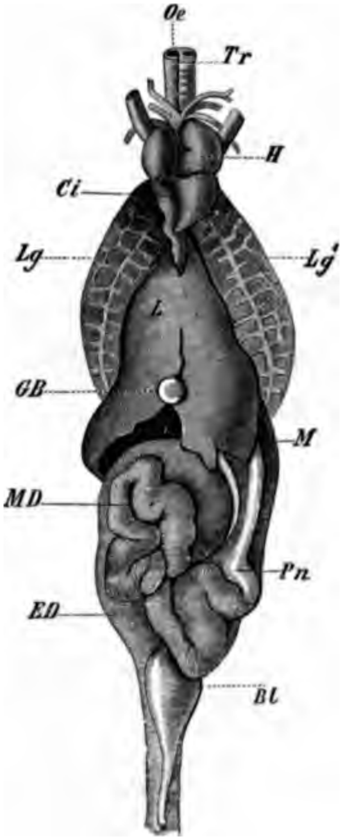

Fig. 255.—Viscera of *Lacerta agilis*.

Bl, urinary bladder; *Ci*, postcaval; *ED*, large intestine; *GB*, gall-bladder; *H*, heart; *L*, liver; *Lg*, Lg^1, the two lungs; *M*, stomach; *MD*, small intestine; *Oe*, œsophagus; *Pn*, pancreas; *Tr*, trachea.

In the Anamnia, the liver is usually relatively larger than in the Amniota, and Carnivores generally possess a larger liver than Herbivores. In Myxinoids it departs least from the original tubular type, from which that of the Amphibia and Reptilia, and more especially the Mammalia, diverges most widely. All these modifications in its structure are traceable, in the first instance, to the vascular system, which has a very specific arrangement in the liver and shows a divergent mode of development in passing towards Amphibians and Reptiles on the one hand, and Mammals on the other.

The liver is connected with the body-wall by folds of the peritoneum, and the differences which are seen in its form are due to the fact that it becomes more or less closely adapted to fit against and between the neighbouring organs (stomach, intestine, &c.), and as regards the formation of lobes, to its close relations with the portal and hepatic veins and (in Mammals) to the diaphragm.

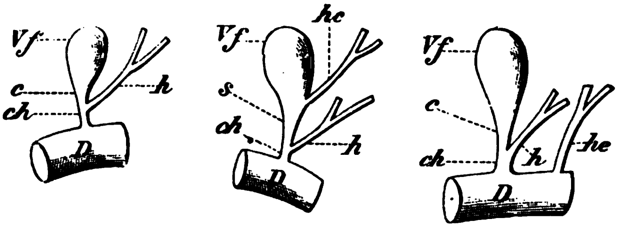

FIG. 256.—A, B, C, VARIOUS MODIFICATIONS IN THE ARRANGEMENT OF THE BILE-DUCTS.

c and *s*, cystic duct; *ch*, common bile-duct; *D*, duodenum; *h*, hepatic duct; *hc*, hepato-cystic duct; *he*, hepato-enteric duct; *Vf*, gall-bladder.

The number of lobes varies, and in Mammals (*e.g.* Carnivores) there may be as many as six or seven.

The function of this large and vascular organ consists, in the first instance, in the secretion of bile, but it has a further importance in connection with the formation of glycogen, urea, &c. It is connected with the lumen of the anterior part of the intestine by means of one or more bile-ducts, an offshoot from which may become enlarged and give rise to a receptacle, the *gall-bladder*. The duct from this is known as the *cystic duct*: it is connected in various ways with the system of *hepatic ducts* from the liver, and thus may form a *common bile-duct* opening into the intestine[1] (Figs. 256, 257).

PANCREAS.

The pancreas arises from the proximal portion of the small intestine, near the liver, in the form of several independent endodermic outgrowths. These are respectively dorsal and ventral in position, and in most Craniates one dorsal and two ventral rudiments can be recognised, of which one or more may undergo reduction or fusion later, so that the number of ducts opening into the intestine varies in the different groups: there may be only one, or there may be several (*e.g.* Birds, Crocodiles, Emydæ, and some Mammals). In some cases the ducts communicate with the bile-duct[1] (Fig. 257).

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[1] On the metamorphosis of the ammocœte-larva of the Lamprey, the single-lobed liver, like the intestine, undergoes a peculiar modification and partial degeneration. It is at first of a typical tubular structure, and possesses bile-ducts and a gall-bladder; the bile-capillaries, ducts, and gall-bladder gradually disappear, and at the same time the blood-capillaries become enlarged and more completely surround the cell-trabeculæ, so that a change of function probably occurs.

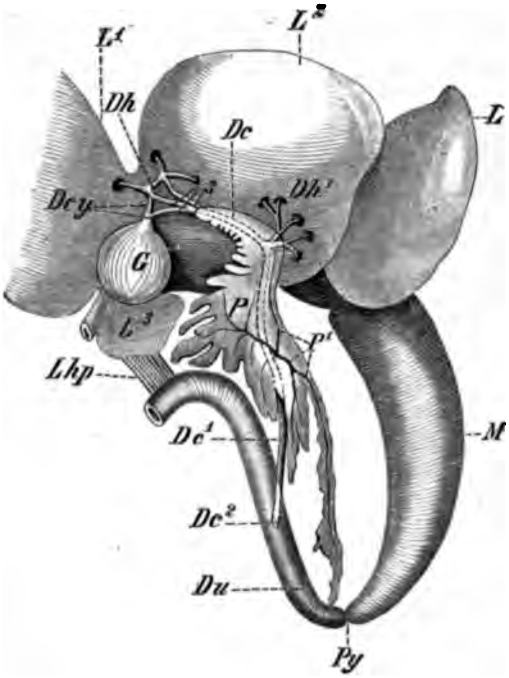

FIG. 257.—PANCREAS AND LIVER OF FROG, TO SHOW THE ARRANGEMENT OF THEIR DUCTS.

Dcy, cystic ducts, which, together with the hepatic ducts (*Dh*), form a network from which three collecting ducts arise, and these unite to form the common bile-duct (*Dc*): the latter passes through the substance of the pancreas (*P*), receiving further hepatic ducts (Dh^1), and the pancreatic ducts (P^1); at Dc^1 it becomes free from the pancreas, and passes back to open into the duodenum (*Du*) at Dc^2; *G*, gall-bladder; *L*, L^1, L^3, the lobes of the liver turned forwards; *Lhp*, duodeno-hepatic omentum; *M*, stomach; *Py*, pylorus.

Varying much in form and size, the pancreas early gives rise to a band-shaped or more or less lobulated and very vascular organ, its greater part usually lying in the fold of the duodenum. In some cases it remains embedded within the wall of the gut (*e.g.* Protopterus, cf. Fig. 247). Amongst Teleosts it may be in part surrounded by the liver: in part, however, it does not form a compact gland, but has the form of scattered lobules extending throughout the mesentery. It is unrepresented in Amphioxus.

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[1] The large digestive glands are said to appear ontogenetically in the following order: 1, liver; 2, dorsal pancreas; 3, ventral pancreas. Phylogenetically the order is: 1, liver (Amphioxus, Cyclostomata); 2, liver and dorsal pancreas (Elasmobranchii); 3, liver, and dorsal + ventral pancreas (most other Vertebrates, including Amphibia, Sauropsida, and Mammalia).

In Petromyzon, a pancreas is developed in the embryo, and is embedded in the wall and spiral fold of the gut and in the dorsal portion of the liver. In Myxine and Bdellostoma also a glandular organ can be recognised in the neighbourhood of the bile-duct, into which its lobules open independently.[1]

[1] The histological structure of this organ in Cyclostomes resembles that of the peculiar "intertubular cell-masses" or "islets of Langerhans" present amongst the ordinary pancreatic tubules of other Vertebrates. These are of epithelial origin, but have no ducts: they probably pour their secretion into the surrounding lymph-vessels and blood-vessels, and may be included under the category of "glands with internal secretion" (cf. p. 247). It has been suggested that the pancreas may represent phylogenetically two distinct glands, the more primitive of which is alone present in Cyclostomes, while in other Vertebrates it has been largely replaced by the pancreas proper.

G. ORGANS OF RESPIRATION.

The typical respiratory organs of Vertebrates are closely connected with the enteric or alimentary canal both as regards position and development, and are of two kinds, **gills** and **lungs.** The former, as the phylogenetically older organs, are adapted for aquatic respiration, and are connected with the pharynx in the region of the visceral clefts: the latter always arise as sac-like outgrowths of the pharynx, which grow backwards so as to lie within the body-cavity.

Both gills and lungs may be developed in the same individual, but are usually not functional at the same time. Both are supplied with venous blood which becomes oxygenated while passing through their capillaries.

The *swim-bladder* or *air-bladder* present in many Fishes, and acting as a hydrostatic organ, arises in a similar manner to the lungs—that is, as an outgrowth from the fore-part of the alimentary tract: it usually receives oxygenated blood from the aorta, and venous blood passes from it into the cardinal, hepatic, or hepatic portal veins; but in some cases (*e.g.* Bony Ganoids and certain Teleosts) it may act as an accessory respiratory organ.

In some cases also the oral and pharyngeal mucous membrane (*e.g.* certain Amphibians), or the intestine (*e.g.* certain Siluroid Fishes), may take part secondarily in respiration, and the integument may be very important in this respect (*e.g.* in Amphibians).

I. GILLS.

The gills arise in connection with a series of laterally-arranged outgrowths of the pharynx lying one behind the other, which become open to the exterior. Passages or clefts separated by septa are thus formed for the water entering by the mouth, and in order that oxygen may become absorbed, leaf-like or thread-like vascular processes, the *internal gills* or *branchiæ*, become developed in the region of each cleft. Apart from these, *external gills* sometimes occur, and in certain cases, both kinds are developed in the same animal.

In the development of the internal or *enteric* gills, the endoderm plays the chief part as the lining or covering layer, the ectoderm being limited to the outer parts of the branchial septa and only being of secondary importance. The true external or *integumentary* gills arise as projections of the surface, covered by ectoderm, at points between which the clefts are subsequently formed, but it has recently been maintained that the endoderm takes part in their formation also.

Fishes possess gills throughout life. Amongst Amphibians this is only the case in the Perennibranchiata: all the others simply pass through a gilled stage, and later nearly always breathe by means of lungs.

Thus the study of this one Order furnishes us with an excellent representation of the course of phylogenetic development through which all the higher Vertebrates must have passed, and which is still indicated in them by the appearance in the embryo of gill-clefts and gill-arches with a corresponding arrangement of the blood-vessels: these occur throughout the entire series of the Amniota—that is, in forms in which they no longer possess a respiratory function.[1]

Amphioxus.—The small mouth leads from the cavity of the oral hood into that of the pharynx, and is provided with a muscular fold, the *velum*. The numerous (80—100 or more) gill-clefts, which are arranged in pairs and supported by elastic cuticular rods, extend backwards nearly to the middle of the body. At first they open freely to the exterior, but at a later period of development they become enclosed by a paired fold of the integument which gives rise to an *atrial* or *peribranchial chamber*, opening by a single pore situated somewhat behind the middle of the body (for details, cf. Fig. 258).

The relative extent of the branchial apparatus is considerably limited, even in the lowest Craniata, as compared with Amphioxus.

Cyclostomes.—In the Ammocœte-larva of the Lamprey the œsophagus is continued directly backwards from the pharynx (Fig. 259, A), and at the anterior end of the latter there is a muscular velum, covered by the mucous membrane (Fig. 260). The seven gill-sacs provided with leaf-like folds of mucous membrane which are present in the Ammocœte, persist in the adult; but, with the formation of a suctorial mouth, the portion of the œsophagus into which they open becomes closed posteriorly, the gullet apparently growing forwards above the latter, and joining the mouth-cavity at the velum. Thus two canals pass

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[1] Thus indications of five or six clefts are seen in the embryos of most Reptiles, and of five in Birds and Mammals; in many cases, however, they do not become open to the exterior. Their order of disappearance is from behind forwards, and the most anterior (mandibulo-hyoid) cleft persists in a modified condition even in the adult, undergoing a change of function in connection with the auditory organ (p. 294). Certain of the anterior arches persist in a modified form (*cf.* under Skull and Larynx).

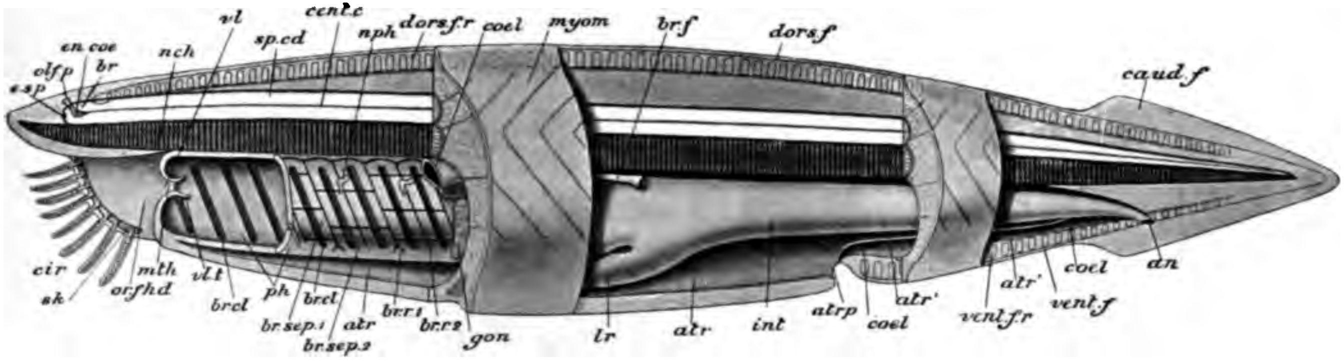

FIG. 258.—DIAGRAM OF THE ANATOMY OF AMPHIOXUS. (From Parker and Haswell's *Zoology*.)

an, anus; *atr*, atrium: *atr'*, its posterior prolongation; *atrp*, atriopore; *br*, "brain"; *br.cl*, branchial clefts; *br.f*, "brown funnel"; *br.sep. 1*, primary, and *br.sep. 2*, secondary branchial lamella; *br.r. 1.* primary, and *br.r. 2*, secondary branchial rod; *caud.f*, caudal fin; *cent.c*, central canal; *cir*, cirri; *coel*, cœlome; *dors.f*, dorsal fin; *dors.f.r*, dorsal fin-rays; *en.coe*, ventricle of "brain"; *e.sp*, eye-spot; *gon*, gonad; *int*, intestine; *lr*, liver; *mth*, mouth; *myom*, myomeres; *nch*, notochord; *nph*, nephridia; *olf.p*, olfactory pit; *or.hd*, oral hood; *ph*, pharnyx; *sk*, skeleton of oral hood and cirri (dotted); *sp.cd*, spinal cord; *vent.f*, ventral fin; *vent.f.r*, ventral fin-rays; *vel*, velum; *vlt*, velar tentacles.

backwards from the mouth, a ventral *branchial* or *respiratory tube*, and dorsal œsophagus (Fig. 259, B). Inspiration as well as expiration takes place through the gill-apertures when the animal is attached by its suctorial mouth.

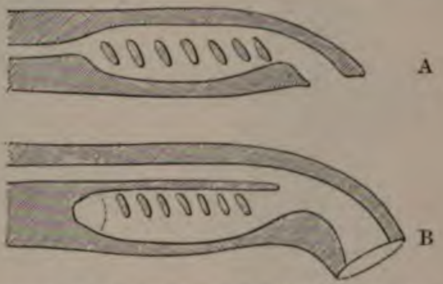

FIG. 259.—DIAGRAM OF A LONGITUDINAL SECTION THROUGH THE HEAD OF THE LARVAL (A) AND ADULT (B) LAMPREY.

In Petromyzon and Bdellostoma[1] the individual branchial sacs, which communicate directly with the pharynx, open freely to the exterior: in Myxine this original condition becomes modified by the outer parts of the gill-passages growing out into long tubes, which unite to form a common duct on either side; this opens far behind the branchial apparatus on the ventral side of the body.

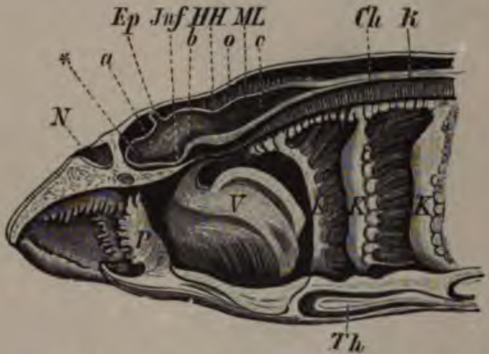

FIG. 260.—LONGITUDINAL SECTION THROUGH THE HEAD OF A LARVAL LAMPREY.

b, *c*, ventricles of the mid- and hind-brain; *Ch*, notochord; *Ep*, epiphysis; *HH*, *ML*, hind-brain; *Jnf*, infundibulum; *K*, *K*, *K*, the three anterior gills; *N*, nasal sac; *o*, subdural cavity; P, papillæ of mucous membrane; R, spinal cord; *Th*, thyroid (hypobranchial furrow); *V*, velum; *, communication between the ventricle of the olfactory lobe and that of the telencephalon.

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[1] In Bdellostoma there are usually six or seven pairs of branchial sacs, and behind these, on the left side, an *œsophageo-cutaneous duct* opens directly into the pharynx, as is also the case in Myxine. Bdellostoma bischoffi and B. stouti possess eleven or twelve, and B. polytrema thirteen or fourteen pairs of gill-pouches.

Fishes.—In the true Fishes the gills come into close relation with the visceral arches, and in Elasmobranchs they consist of closely approximated transverse laminæ, which are firmly attached to both sides of the septa extending outwards from the arches and separating the individual gill-sacs from one another, so that each septum bears a half-gill, or *hemibranch*, on both its anterior and posterior surface (Figs. 261, A, and 262). A gill, or *holobranch*, thus consists of the branchial septum and arch *plus* the posterior hemibranch of the sac in front of it and the anterior hemibranch of the following sac. The gill-sacs, of which there are commonly five in Plagiostomes,[1] open separately to the exterior, and a vestigial

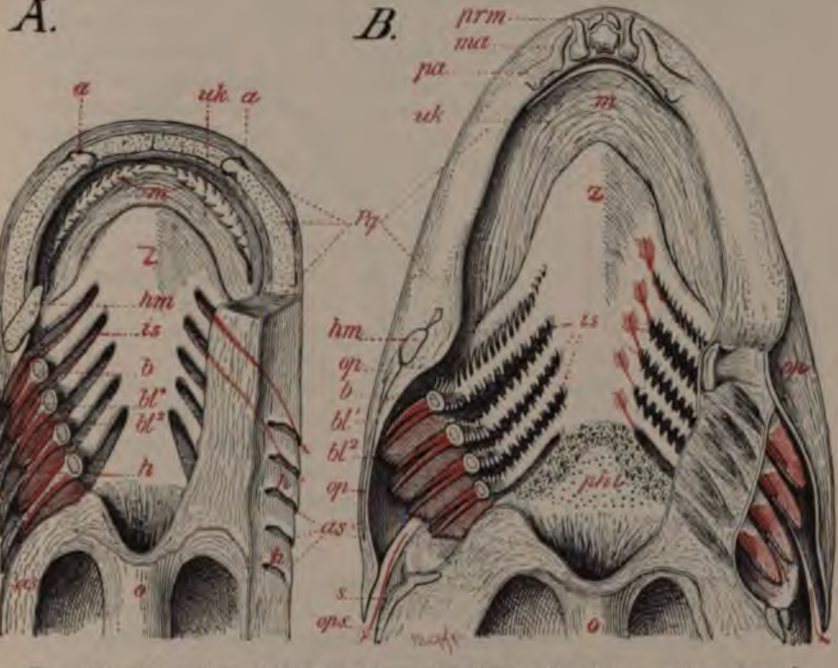

Fig. 261.—Dissection of the head from the dorsal side of A, an Elasmobranch (*Zygæna malleus*), and B, a Teleost (*Gadus æglefinus*), to show the branchial apparatus. In both figures the branchial arches on the left side are shown cut through horizontally. (From R. Hertwig's *Zoology*.)

as, external branchial apertures; *b*, branchial arch; *bl*¹, *bl*², hemibranchs; *h*, branchial septum; *hm*, hyomandibular; *is*, internal branchial apertures and gill-rakers; *m*, oral cavity; *ma*, maxilla; *o*, œsophagus; *op*, operculum; *ops*, opercular aperture; *pa*, palatine; *phi*, inferior pharyngeal bone; *Pq*, palatoquadrate, and *a*, its connection with the cranium anteriorly; *prm*, premaxilla; *s*, pectoral arch; *uk*, lower jaw; *z*, tongue.

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[1] There are six in Hexanchus and Chlamydoselachus and seven in Heptanchus in addition to the spiracle.

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gill-cleft known as the *spiracle* (p. 88), is nearly always present more anteriorly, between the mandibular and hyoid arches. In the Holocephali the spiracle is wanting, and there are only four clefts and three holobranchs in addition to hemibranchs on the hyoid and fourth branchial arch ; moreover, an opercular membrane is present, covering the external branchial apertures and opening by a slit posteriorly. In Chlamydoselachus fringed folds from the hyoid and interbranchial septa project over the clefts.

In Ganoids and Teleosts there are no longer chambered gill-sacs. The septa on which the gill-laminæ are borne become greatly reduced, so that the apices of the latter extend freely outwards ; the whole branchial region is, moreover, covered over by the operculum and branchiostegal membrane (cf. pp. 89 and 94), and thus, as in the Holocephali, the gill-slits open into a common branchial chamber, which communicates with the exterior by a single slit-like aperture on either side (Figs. 261, B, and 262). A spiracle is present in Acipenser, Polyodon, and Polypterus amongst Ganoids.

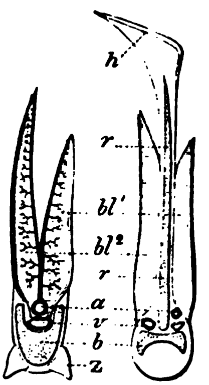

FIG. 262. — TRANSVERSE SECTION THROUGH A HOLOBRANCH OF *Zygæna* (ON THE RIGHT) AND *Gadus* (ON THE LEFT). SLIGHTLY ENLARGED. (From R. Hertwig's *Zoology*.)

a, afferent, and *r*, efferent branchial vessels ; *b*, branchial arch ; bl^1, anterior, and bl^2, posterior hemibranch of the gill; *h*, septum ; *r*, cartilaginous gill-ray ; *z*, gill-rakers.

The mechanism of respiration in Teleosts is as follows. In inspiration, an expansion of the oral cavity takes place by the opercular apparatus being raised, the branchiostegal membrane at the same time moving inwards so as to close the opercular slit. An elastic, valve-like fold of the mucous membrane, enclosing numerous smooth muscle-elements, is present in the maxillary region projecting downwards from the roof of the mouth, and a similar fold arises from the floor of the mouth in the mandibular region. On the expansion of the oral cavity and closure of the branchiostegal valve, the pressure of the water causes the maxillary and mandibular valves to open inwards, and thus to admit the inspiratory current (Fig. 263, A). The movements of expiration then follow by the contraction of the opercular apparatus, which causes the water in the mouth to press on the maxillary and mandibular valves and thus close them, while the branchiostegal valve is opened (B). Thus the mechanism of these valves is quite similar to that of the valves of the heart, and the respiratory current is produced by the contraction of the walls of the mouth, which act like a pump.

As a rule Teleosts possess only four holobranchs,[1] and this holds good for all Ganoids. A vestigial gill or *pseudobranch* is present on the anterior wall of the spiracle of many Elasmobranchs and of cartilaginous Ganoids (*mandibular pseudobranch*); the posterior hyoid hemibranch, which is functional in Acipenser and Lepidosteus, becomes more or less reduced in other Ganoids and Teleosts, forming the so-called *opercular pseudobranch*. Traces of a cleft, lying behind the functional branchial clefts, are found in the embryos of certain Fishes and Amphibians. All these facts indicate the presence of a more extensive branchial apparatus in ancestral forms. (For the sieve-like *gill-rakers*, cf. Figs. 261 and 262.)

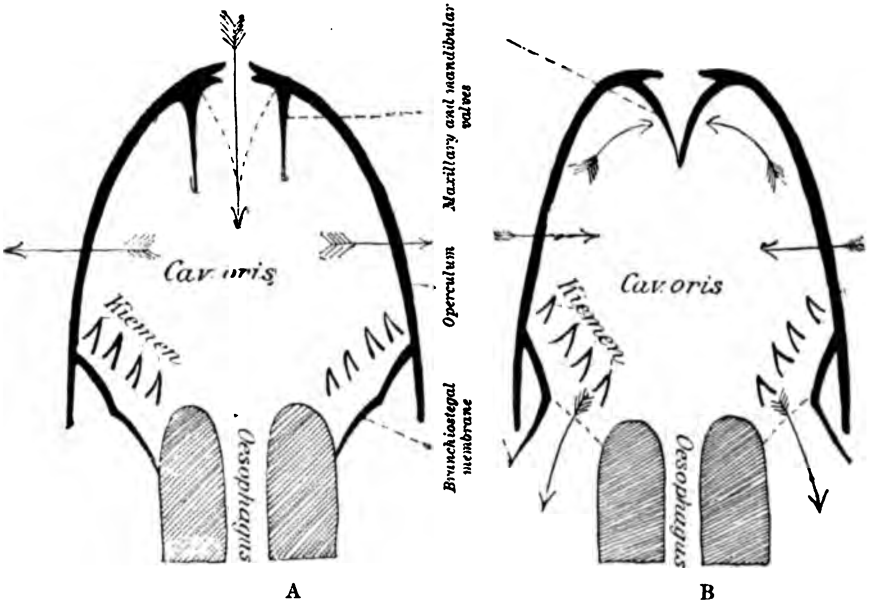

FIG. 263.—DIAGRAM ILLUSTRATING THE MECHANISM OF RESPIRATION IN TELEOSTS. (After Dahlgren.)

A, phase of inspiration; *B*, phase of expiration. In both figures the anterior oral part (*cav. oris*) represents a vertical section, and the posterior pharyngeal part enclosing the gills (*Kiemen*) a horizontal section. The arrows indicate the direction of the water-current and pressure, and those passing through the walls of the oral cavity the expansion and contraction of the opercular apparatus. In *A*, the maxillary and mandibular valves are open, and the branchiostegal membrane closed: in *B*, this condition is reversed.

In the Lophobranchii the gills are replaced by tufted processes, and in many Teleostei certain accessory structures are developed in the posterior region of the branchial chamber by a modification of the branchial cavities and skeleton.[1] These serve to retain water and air, and thus the Fish is able to breathe for some time out of the water (Anabas, Saccobranchus, Heterobranchus, Clarias).

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[1] They may be reduced to three, or two, and even these may be more or less rudimentary.

The Dipnoi, as their name implies, possess both gills and lungs, the latter alone being functional in Protopterus and Lepidosiren during the torpid period (p. 20). The internal gills are covered by a small operculum. In Ceratodus there are four holobranchs on the first four branchial arches as well as a "hyoid hemibranch" (which perhaps belongs to the first branchial arch); the gill-lamellæ extend round the clefts, so that the hemibranchs of each cleft are continuous. In Protopterus and Lepidosiren a reduction of these organs has taken place, gills being absent in the former genus, for example, on the first and second branchial arches; there is, however, in addition, an anterior hemibranch on the fifth branchial arch.[2]

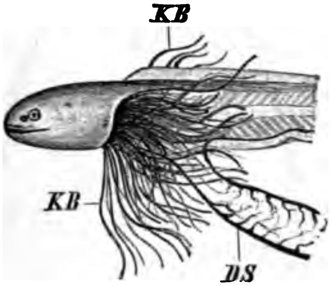

FIG. 264.—EXTERNAL GILLS OF LARVA OF *Gymnarchus niloticus*, 4 DAYS AFTER HATCHING. (After J. S. Budgett.)

DS, yolk sac ; *KB*, external gills.

In embryos of Elasmobranchs and certain Teleosts (Heterotis, Gymnarchus, Fig. 264), long, vascular, thread-like "external gills" arise from the endoderm of the clefts and extend backwards over the body. In the larval Polypterus and Calamichthys there is a single true (integumentary) external gill on either side in the hyoid region, which differs markedly from those just described, and consists of a main stem giving off a double row of filaments and supported at its base by cartilage (Fig. 265, *b*). In larvæ of Protopterus and Lepidosiren somewhat similar external gills are present, but are four in number on either side and are situated on the branchial arches (Fig. 265, *a*). Of these, vestiges of the three upper ones persist in Protopterus even in the adult.

Amphibians.—In the embryos of Urodeles, indications of five gill-clefts can usually be recognised, but the most anterior (hyomandibular) cleft, as in other Amphibians, does not become open to the exterior: they are covered over by an opercular-like fold of the skin, thus leaving only a single aperture externally. In the larvæ, as well as in adult Perennibranchiates, there are three external gill-tufts in connection with the three anterior branchial arches, lying one over the other; these extend backwards, projecting freely to the exterior, and are unsupported by cartilage. Each consists of a main axis with secondary branches, so that the gills have the form of tufts or delicately branched structures

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[1] Other parts may also become modified to serve as accessory respiratory organs. Thus in Cobitis and Callichthys intestinal respiration takes place ; and in Monopterus javanensis (which, like Protopterus and Lepidosiren amongst the Dipnoi, passes through a torpid period in holes in the ground during the dry season) buccal, pharyngeal, and intestinal respiration occur, and interesting modifications of the blood vessels are seen.

[2] Cf. Note on p. 97. There are five clefts in Ceratodus and Protopterus, and four in Lepidosiren. It is probable that the hyobranchial cleft is closed in Protopterus, as is the case in Lepidosiren; the spiracular cleft does not become perforated in the embryo.

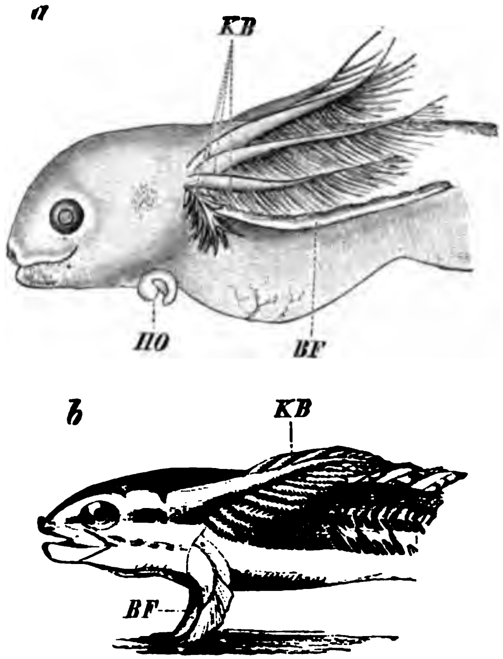

Fig. 265.—Larvæ of (*a*) *Protopterus annectens* (17 Days after Hatching) and (*b*) *Polypterus lapradei* (1¼ in. long, × about 4). (After J. S. Budgett.)

BF, pectoral fin; *HO*, sucker, or cement organ; *KB*, external gills (single in Polypterus).

showing the most varied arrangements for increasing the respiratory surface (cf. Fig. 266). These external gills must not be confused with the internal gills, which are wanting in all Urodeles. They are acted on by a complicated system of muscles and are covered by ciliated epithelium, which serves to keep up a continual current in the surrounding medium.

The gills are lost at metamorphosis in the Derotremata and Myctodera. In larval Myctodera, as mentioned above, there are five open clefts, all of which disappear at metamorphosis. In the

Perennibranchiata, the most anterior (hyobranchial) cleft becomes closed in Siren; in Necturus, Proteus, and Typhlomolge, the most posterior also disappears, while in the Derotremata (*e.g.* Amphiuma) only one remains, viz. that between the third and fourth arches, and this not in all cases. In this respect, therefore, the Myctodera are the most primitive, and there is every reason for assuming that the Perennibranchiata, though retaining certain larval characters, have been derived from caducibranchiate forms.

In Anuran larvæ, the three pairs of external gills are less complicated than those of Urodeles (cf. Fig. 266), and are soon replaced by internal gill-tufts situated in the three branchial clefts.[1] By the growth of opercular folds, which contain no skeletal parts, the external respiratory aperture of either side becomes gradually reduced in size, and the two branchial chambers usually open eventually by a single aperture, which is situated either in the median ventral line (Bufo, Bombinator) or laterally (Rana). The larvæ of the Gymnophiona also possess external gills, which in Epicrium glutinosum, for example, are feather-like.[2]

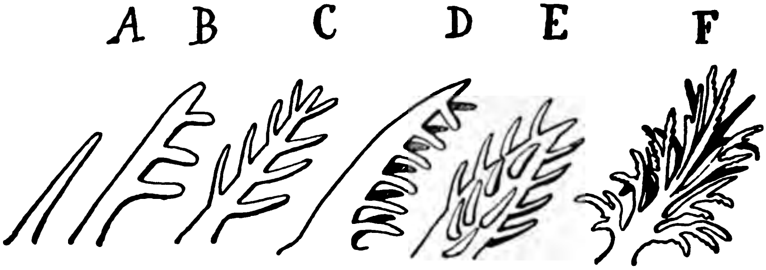

FIG. 266.—DIAGRAM ILLUSTRATING THE DEVELOPMENT OF THE AMPHIBIAN GILL. (Mainly after P. Clemens.)

A, rod-like, unbranched, primitive form, retained in the adult of certain Anura (*e.g.* Xenopus). B, form in which there is only a single series of branches (Anura). C, feather-form, with two opposite series of branches (Derotremata: this form is also primarily met with in the Gymnophiona and in embryos of Myctodera). D, wedge-shaped, unbranched axis, on the lower border of which the gill-filaments arise in rows (embryos of most Urodeles). E, leaf-like, unbranched axis, on which the filaments increase in number, and are arranged in four rows on the surface as well as on the edges (Axolotl-stage of Amblystoma, Necturus). F, branched axis (Proteus, Siren).

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[1] The so-called internal gills of Anura are said to correspond to a series of outgrowths from the bases of the external gills, and thus not to be comparable with the endodermal gills of Fishes.

[2] The external gills of Amphibia present a great variety of form, often resulting from adaptation. Thus, in the intra-uterine larvæ of the viviparous Salamandra atra, they reach a length of 5–6 centimetres; in Cæcilia compressicauda they consist of two large, flattened, vascular folds, which apparently cover the body of the larva like a mantle; and in Notodelphys (Nototrema) amongst Anurans, in which the larvæ undergo development in the pouch on the back of the mother, they are bell-shaped and stalked. In certain other Batrachians in which there is no free larval stage, it appears that respiration may take place before hatching by means of the broad and vascular tail (Hylodes

II. SWIM-BLADDER AND LUNGS.

1. THE SWIM-BLADDER.

As already mentioned (p. 351), the lungs and swim-bladder are developed in a similar manner, and only differ from one another in the fact that the former always arise from the ventral side of the pharynx, and the latter usually on the dorsal side. The various attempts which have been made to trace the phylogenetic connection between swim-bladder and lungs have so far not been completely successful. It has been supposed that the dorsal origin of the former has come about by a process of rotation: on the other hand, it may be that the two organs are not strictly homologous, each having arisen independently from a similar outgrowth at a different point in the alimentary tube. In this case, the so-called swim-bladder of Polypterus would be directly comparable to the lungs of Dipnoans and higher forms rather than to the swim-bladder of other Fishes.

The exact point of origin of the swim-bladder from the alimentary canal varies,[1] and its duct (*ductus pneumaticus*) may either remain open throughout life, as in Ganoids and some Teleosts (*Physostomi*), or it may later become reduced to a solid fibrous cord or even entirely obliterated, as in other Teleosts (*Physoclisti*). In the latter case there is no communication between the swim-bladder and the external air, and the contained gas must therefore be given off from the walls of the swim-bladder itself: this has been shown to be the case amongst Physostomi also. In certain of the latter, vascular "red-bodies" are present; in others and in the Physoclisti, gland-tubules are present amongst the vascular networks or "retia mirabilia," and the number, relative size, and position of these *gas-glands* varies in different forms. Diffusion of gas (probably mainly oxygen) into the bladder takes place in certain thin, oval regions lined by a flat epithelium and provided with regulating dilator and sphincter muscles.

A swim-bladder is wanting in Amphioxus, Cyclostomes, and Elasmobranchs, and in other Fishes varies much in form and in its relations to surrounding parts (alimentary canal, blood-vessels skeleton). As a rule, it lies above the peritoneum on the dorsal side of the body-cavity, between the vertebral column, aorta, and kidneys on the one hand, and the alimentary canal on the other, and is invested by the peritoneum on the ventral side only. It is

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martinicencis) or folds of the body-wall (Rana opisthodon). In Xenopus, the branched tentacles at the angles of the mouth are said to have a respiratory function, and, like the "balancers" of Urodeles (cf. note on p. 271), may correspond morphologically to the external gill of the first visceral arch.

[1] In Erythrinus it arises laterally, and in some Physostomi (*e.g.* Herring) it opens further back, into the stomach.

more or less sac-like in form, is only exceptionally paired, and usually extends along the whole length of the body-cavity; its walls are composed of connective, elastic, and muscular tissue.[1] In some Teleostei the swim-bladder is transversely constricted so as to form several successive divisions; in other cases it may give rise to a more or less numerous series of cæcal processes. Its internal surface may be either smooth or spongy (Fig. 267) owing to the formation of a meshwork of trabeculæ, the structure of which resembles that of the lungs of Dipnoi and Amphibia, and, as already stated, it has a respiratory function in some cases.

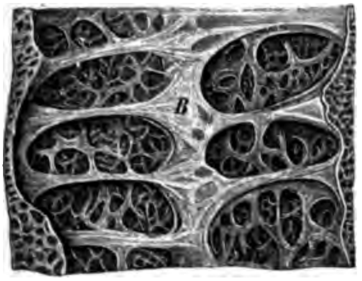

FIG. 267. — INTERNAL SURFACE OF THE AIR-BLADDER OF LEPIDOSTEUS, SHOWING THE TRABECULÆ.

B, fibrous longitudinal band.

Attention has already been directed to the relations which may exist between the swim-bladder and the auditory organ (cf. p. 297).

2. THE LUNGS.

The lungs arise at the hinder border of the branchial region of the pharynx. Their phylogenetic history is not clear, and the view that they arose primarily from visceral clefts does not seem to be a very probable one.

On the first appearance of the lung-rudiments, the pharynx becomes laterally compressed immediately above the fifth or sixth arterial arch, and divided by a longitudinal horizontal fold into a dorsal and a ventral portion, the latter of which gives rise to a blind sac, opening anteriorly by a wide aperture into the former and lined by endoderm (Fig. 268). A longitudinal vertical furrow is then formed, dividing this primitive lung-sac into right and left halves: the narrower proximal portions of these represent the primitive *bronchi*, which communicate with the pharynx by a short tube, the primitive windpipe or *trachea*. The proximal end of the latter subsequently becomes differentiated to form a *larynx*, or organ of voice, which opens into the pharynx on its ventral side by means of a slit-like aperture, the *glottis*. The lungs are therefore phylogenetically older organs than the bronchi, trachea, and larynx, and this fact is supported by a study of their comparative anatomy.

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[1] In Dactylopterus volitans, the two halves of the swim-bladder extend beyond the general cœlome into special cavities, and the organ is covered by large bony plates. In the Gymnodonts (*e.g.* Diodon, Tetrodon), the whole œsophagus is capable of great distension.

Hollow outgrowths and buds arise from the endoderm lining

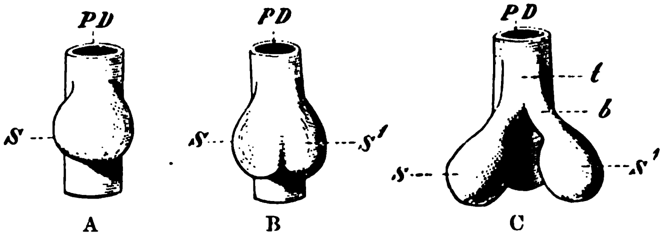

FIG. 268.—A, B, C, DIAGRAMS SHOWING THE MODE OF DEVELOPMENT OF THE LUNGS.

b, bronchus; *PD*, primitive alimentary tube; *S*, S^1, the lung-sacs, which are at first unpaired; *t*, trachea.

the primary central cavity ("intrapulmonary bronchus") of each lung: these extend into the surrounding vascular mesoderm, which

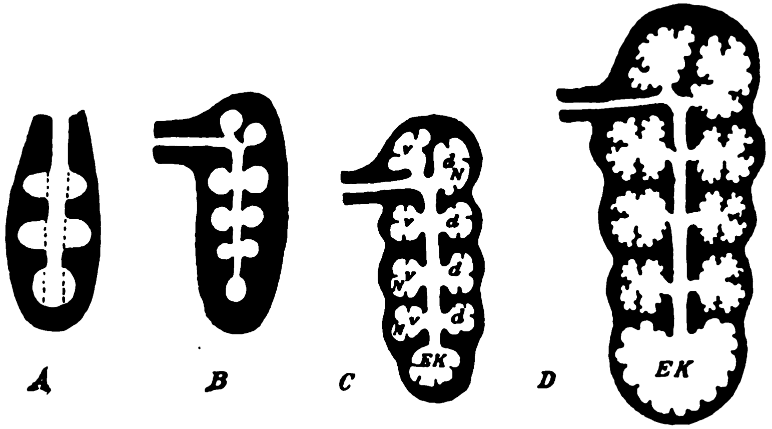

FIG. 269.—DIAGRAMS ILLUSTRATING THE BUDDING OF THE BRONCHI IN THE DEVELOPING LUNG OF EMYS. (After Fanny Moser.)

A, buds from the intrapulmonary bronchus are shown extending into the lung-wall. B. The intrapulmonary bronchus, which still forms a narrow tube extending through the whole length of the lung, has given off a number of primary pulmonary vesicles extending into the thick wall of the latter. C. By a marked thinning-out of the lung-wall, the vesicles form chambers, of which four dorsal (*d*) and four ventral (*v*) are visible, each of which has developed secondary buds (*N*); the bronchus itself has become enlarged and given rise to a terminal chamber (*EK*). D. Lung of adult. The chambers have become enlarged and are separated from one another merely by narrow septa, corresponding to the reduced lung-walls: the secondary buds have given rise to buds of a third order, which form the lung-crypts, and the terminal chamber (*EK*) is enlarged.

gives rise to muscular fibres and connective tissue, and thus a branched system of cavities communicating with the bronchi is gradually formed (secondary and tertiary bronchi, &c.). The ends of these branches are swollen, forming crypts known as *infundibula*, which are made up of a number of *alveoli* and are surrounded by blood-capillaries, through the thin walls of which the interchange of respiratory gases takes place (Figs. 269 and 270). The bronchi are lined by ciliated epithelium, the infundibula and alveoli by pavement epithelium.

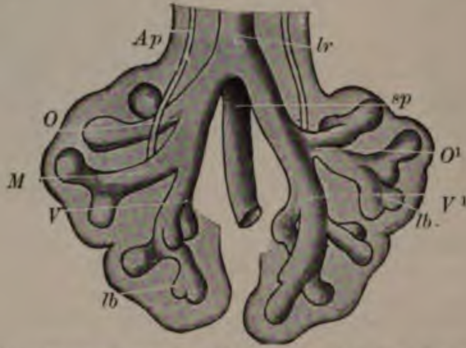

FIG. 270.—DIAGRAM OF THE EMBRYONIC HUMAN LUNG, × 50. (After W. His.)

Ap, pulmonary artery; *lb*, pulmonary vesicle undergoing division; *lr*, air-passage; *M*, middle lobe of the lung; *O*, right anterior upper lobe with its "eparterial" bronchus; O^1, left anterior lobe with its "hyparterial" bronchus; *sp*, œsophagus; *V*, V^1, right and left posterior lobe.

Thus a great increase in the respiratory surface is gradually produced in the ascending series of Vertebrates and in the individual development of the higher forms, in which the lungs may also become secondarily divided up into *lobes*.

In the following account the air-tubes will be dealt with separately from the lungs proper.

Air-Tubes and Larynx.

The walls of the air-tubes may consist, in addition to their lining of ciliated epithelium, of connective tissue and elastic and muscular fibres only, but as a general rule cartilaginous elements are also formed, and these serve to keep the tubes permanently open. From the Amphibia onwards the most anterior of these cartilages, which support the larynx, become differentiated to form a frame on which are stretched the structures by means of which the voice is produced—the *vocal cords*: these cartilages are acted upon by muscles. The relative length of the windpipe as a general rule corresponds with that of the neck.

In certain Fishes there may be a more or less complicated arrangement of the muscles derived from those of the gill-arches (dilator, constrictor, protractor, and retractor) around the aperture of the swim-bladder, though no cartilaginous elements are formed (Fig. 271): these muscles are innerved by the vagus, whether the aperture is dorsal (Lepidosteus, Amia) or ventral (Polypterus). The same is true of the Dipnoi, in which there is a tongue-shaped supporting plate composed of dense connective tissue anteriorly to the glottis, which leads into a muscular vestibule or "laryngo-tracheal" chamber communicating with the lung; but it is doubtful whether this plate can be regarded as the first phylogenetic indication of the laryngeal skeleton of higher forms, and whether the laryngeal muscles of the Amphibia have been derived from those represented in the Dipnoi.

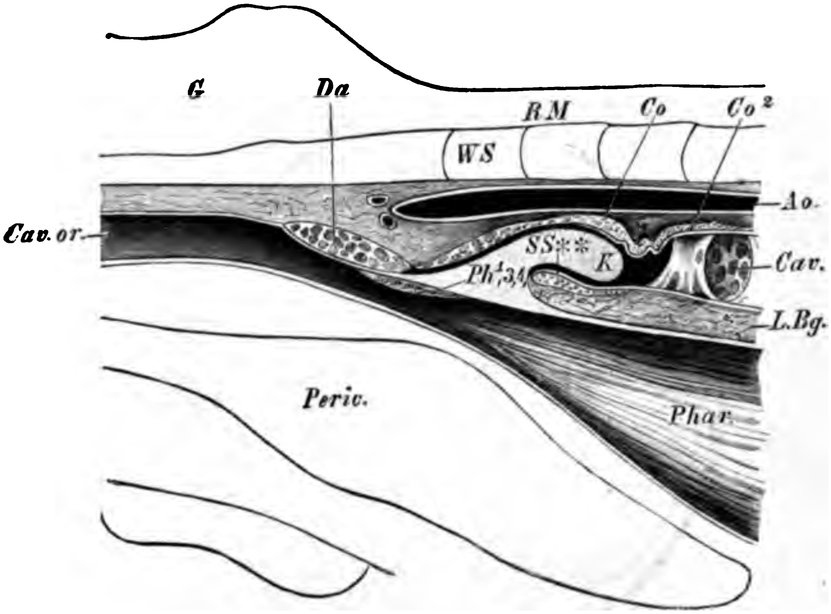

FIG. 271.—MEDIAN LONGITUDINAL SECTION THROUGH PART OF THE HEAD AND TRUNK OF *Lepidosteus osseus*.

Ao, aorta; *Cav*, cavity of the swim-bladder; *Co*, Co^2, and **, constrictors of the pharynx, "larynx," and swim-bladder; *Da*, dilator; *G*, cranial cavity; *K*, cushion-like elevation of the supporting elements of the larynx; *L.Bg*, loose connective tissue between the swim-bladder and pharynx; *Peric*, pericardium; Ph^1, 3, 4, intrapharyngeal branchial muscle; *Phar*, pharynx; *R.M*, neural canal; *SS*, fibrous laryngeal supporting elements; *WS*, vertebral column.

A comparison of these parts in Ganoids and Dipnoans indicates the possibility of the former existence in the vertebrate series of two larynges, a "dorsal" and a "ventral" (Fig. 272), traces of the former of which can still be recognised in Lepidosiren in addition to the ventral larynx.

Amphibians.—The vestibule, or *laryngo-tracheal chamber*, communicates with the pharynx on the one hand and with the lungs on the other, and is supported by definite cartilages; it is provided with intrinsic (dilator and constrictor) and extrinsic muscles, the former derived from pharyngeal muscles, and the latter from trunk-muscles, as in all the higher forms. A definite trachea is differentiated in Siren, Amphiuma, and the Gymnophiona only; it reaches a length of 4 to 5 or more centimetres, and its wall is strengthened by a series of small, irregular cartilages, which usually tend to unite into bands (Fig. 273): only in the Gymnophiona, however, do these bands begin to take on the form of half-rings, and to surround the trachea more or less completely.

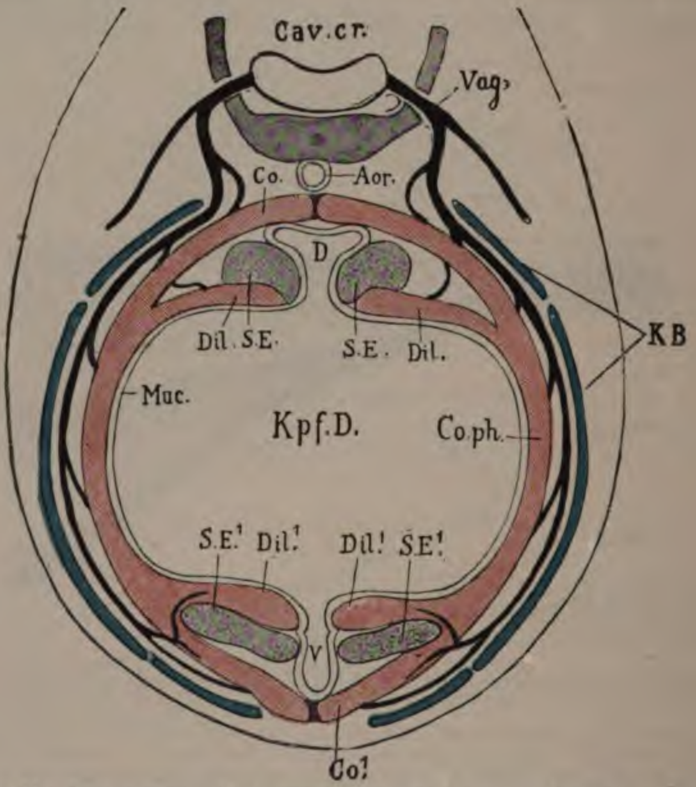

FIG. 272.—DIAGRAMMATIC TRANSVERSE SECTION ILLUSTRATING THE STRUCTURE AND RELATIONS OF THE DORSAL AND VENTRAL LARYNX.

Aor, aorta: *Cav.cr*, cranial cavity; *Co*, *Co*¹, constrictor of the dorsal and ventral larynx respectively; *Co.ph*, constrictor of the pharynx; *D*, dorsal larynx; *Dil*, *Dil*¹, dilator; *KB*, branchial arch; *Kpf.D*, lumen of pharynx; *Muc*, mucous membrane of pharynx; *SE*, *SE*¹, supporting elements; *V*, ventral larynx; *Vag*, vagus nerve.

The primary skeletal parts are a pair of *lateral cartilages*, situated in the walls of the vestibule on either side of the glottis; these appear to have arisen phylogenetically by a modification of the vestige of a branchial arch (possibly the sixth), as is indicated by the innervation of this region by a branch of the vagus. The most primitive form of this lateral cartilage has probably been retained in the caducibranchiate Ellipsoglossa. In various other Urodeles it becomes further developed in various ways, chiefly by its anterior section being differentiated into an *arytenoid cartilage*, while its posterior section gives rise to the *crico-tracheal skeleton* (Fig. 273). The latter gradually becomes more and more closely adapted to the walls of the air-passages, and eventually extends along the whole length of the trachea, its elements passing more or less completely around the windpipe, so that in some higher forms they give rise to completely closed tracheal rings.

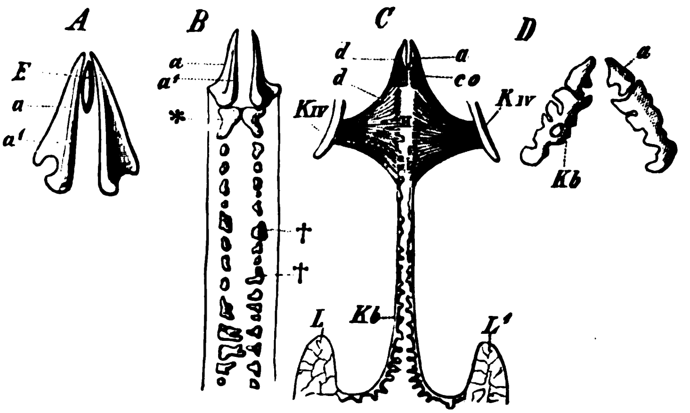

FIG. 273.—LARYNGEAL AND TRACHEAL SKELETON OF URODELES. A, *Necturus* B, *Siren lacertina*; C, *Amphiuma*; D, *Salamandra maculosa.*

a, the lateral cartilages (arytenoids) on either side of the glottis; *a'*, ridge for muscles; *co*, constrictor of the larnyx; *Kb*, the more definite tracheal cartilaginous tracts in Amphiuma and Salamandra; K^{IV}, fourth branchial arch, from which the dilator (*d*) of the trachea and larynx arises: it is inserted into an aponeurosis at *H*; *L*, *L'*, lungs; *, the representative of the cricoid cartilage; ††, cartilages of the trachea in Siren.

The anterior end of the crico-tracheal skeleton in Urodeles gives rise to a very simple ring-shaped *cricoid* cartilage, which, like the rest of the larynx, is much more highly differentiated in Anurans. In these the larynx is regulated by a well-developed series of muscles, and is provided with *vocal cords*, the sound produced by which is often intensified by the presence of vocal sacs developed from the floor of the mouth. The laryngo-tracheal chamber lies between the posterior cornua of the hyoid (thyrohyals), with which it is connected by ligaments, and is supported by a thin arytenoid cartilage on either side of the glottis as well as by a ring-shaped cricoid cartilage, from which delicate processes pass backwards to the roots of the lungs (Fig. 274). Vocal cords are developed in the Anura only, each being attached to the inner concave surface of the corresponding arytenoid.

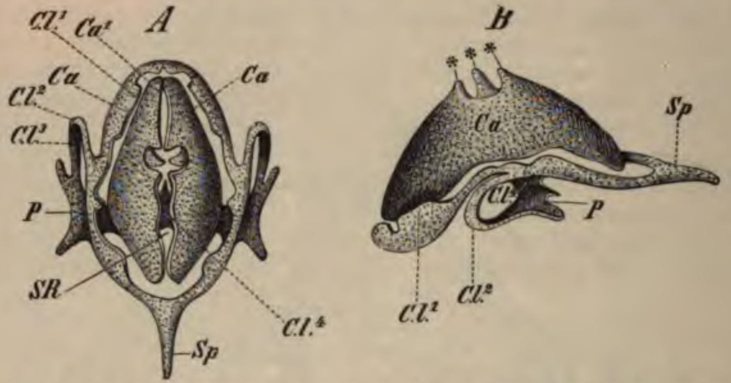

FIG. 274.—CARTILAGINOUS SKELETON OF THE LARYNGO-TRACHEAL CHAMBER OF *Rana esculenta*. A, from above; B, from the side.

Ca, *Ca*, arytenoid cartilages; $C.l^1$—$C.l^4$, cricoid cartilage; *P*, plate-like ventral part of the cricoid; *Sp*, pointed process of the cricoid; *SR*, glottis; ***, three conical prominences of the arytenoids.

The intrinsic laryngeal muscles of Amphibians, which are supplied by a branch of the vagus and are important in respiration (as well as in the production of the voice in Anura), include a

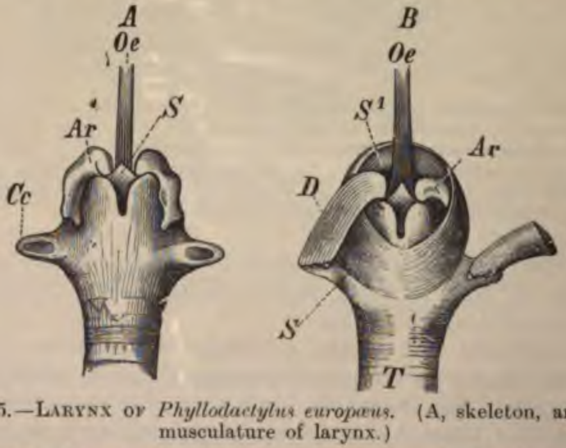

FIG. 275.—LARYNX OF *Phyllodactylus europæus*. (A, skeleton, and B, musculature of larynx.)

Ar, arytenoids; *Cc*, cricoid; *D*, dilator; *Oe*, entoglossal; *S*, anterior median process of cricoid; S^1, sphincter; *T*, trachea.

dilator and one or more constrictors of the glottis. A differentiation of these into distinct pharyngeal and laryngeal muscles occurs only in higher forms.

Reptiles.—The cartilaginous rings of the trachea gradually become more solid and complete in Reptiles, and as in other Amniota are well developed, though not always complete dorsally. The length of the windpipe varies according to the length of the neck and to the point at which it bifurcates into the two bronchi, cartilages being present in these also, and gradually extending along their intrapulmonary portions.

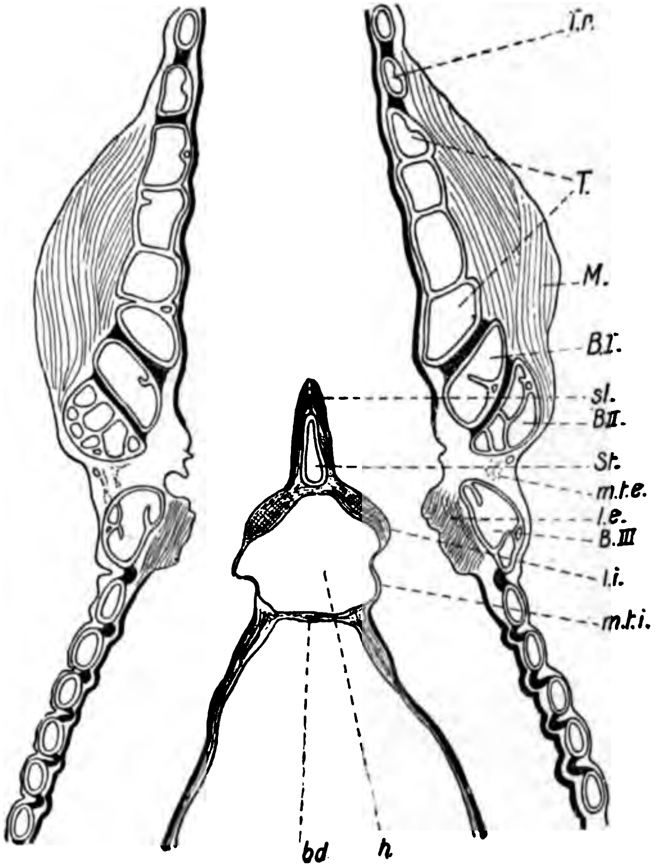

FIG. 276.—SECTION THROUGH THE SYRINX OF A MALE BLACKBIRD (*Turdus merula*). (After V. Häcker.)

bd, brochidesmus; *B.I—III*, 1st–3rd bronchial ring; *h*, ventral cavity (part of the anterior thoracic air-sac); *l.e* and *l.i*, external and internal labia; *M*, muscles; *m.t.e* and *m.t.i*, membrana tympaniformis externa and interna; *sl*, membrana semilunaris; *St*, pessulus; *T*, "tympanum"; *T.r*, tracheal rings.

The cricoid is much more sharply differentiated than in Amphibians, and may give off processes; with it the arytenoids are movably connected.[1] Dilator and sphincter muscles (Fig. 275) are present much as in Urodeles, and as in Mammals, are supplied by two branches of the vagus—an anterior (corresponding to the first branchial branch of Fishes) and a posterior (recurrent), the homologue of that present in Urodeles and of the fourth branchial branch.

Except in Snakes, in which considerable reductions of the hyoid apparatus occur (p. 117), a close connection obtains between the latter and the larynx; in Crocodiles and Chelonians, for instance, the larynx is firmly embedded in a shallow depression on the dorsal surface of the basi-hyoid (Fig. 85). Moreover, the larynx becomes shifted further forwards towards the nasal air-passage. On the whole, however, no considerable advance of the larynx as an organ of voice is seen as compared with that of Amphibians.

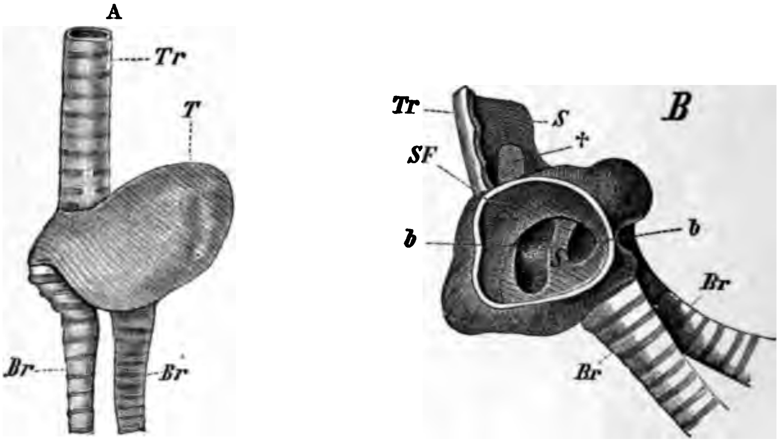

FIG. 277.—LARYNX OF MALE DUCK. *A*, external, and B, internal view.

Br, bronchus; *S*, pessulus, from which a lateral outgrowth (*S*, between *b* and *b*) extends into the tympanum, thus dividing its aperture into the trachea into two portions (*b*, *b*); the aperture is further diminished by the circular fold of mucous membrane, *SF*; *T*, the "tympanum"; *Tr*, trachea; †, thin region in pessulus.

Birds.—In Birds there are two larynges, an *upper* (anterior) and a *lower* (posterior). The former lies in the usual position behind the tongue on the floor of the pharynx, and is plainly homologous with that of other Vertebrates, though it has become reduced and is incapable of producing sound.

The lower larynx, or *syrinx*, is of much greater importance; it is usually situated at the junction of the trachea and bronchi, or more seldom at the lower end of the trachea alone or on the bronchi alone. It serves as the organ of voice, and appears first in, and is restricted to, Birds. In the most usual form (*broncho-tracheal syrinx*), there is a movable connection between the most anterior bronchial rings, with which a complicated system of muscles is connected; these, by their contraction, cause a stretching or relaxing of certain vibratory membranes. A bar of cartilage or bone, the *pessulus*, extends from the junction of the bronchi into the more or less swollen "*tympanum*" at the base of the trachea[1]: this supports a slight fold of the mucous membrane called the *membrana semilunaris*, while the membranous inner wall of each bronchus is known as the *membrana tympaniformis interna:* the external wall may also give rise to a *membrana tympaniformis externa.* The tympanum, which is strengthened by fused tracheal rings, attains a relatively enormous development in some Water-Birds (*e.g.* the male Duck), where it gives rise to a bony vesicle which serves as a resonance cavity (Fig. 277).

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[1] In some Reptiles (*e.g.* certain Lizards and Chelonians) a structure is present which to some extent recalls the epiglottis of Mammals.

All the muscles of the syrinx are derived from the sterno-hyoid group, *i.e.* from the cervical continuation of the rectus-system: this is indicated by their innervation from hypoglossal and cervical elements (Fig. 278). They are thus derivatives of the trunk-muscles, and are therefore fundamentally different from the laryngeal muscles, which have arisen by a modification of the pharyngeal muscles, *i.e.* are of visceral origin.[2]

The relative length of the trachea varies greatly in different Birds, and its complete cartilaginous rings usually become calcified or ossified.[3]

Mammals.—The larynx of Mammals is distinguished from that of all other Vertebrates by the marked differentiation of the muscles—the constrictors always exceeding the dilators in number,—and by the constant presence of an *epiglottis* and a *thyroid cartilage.*

The thyroid cartilage is derived from part of the fourth and fifth visceral arches (cf. Fig. 279), and is closely connected with the hyoid-apparatus: in Monotremes, in which alone it is paired, this connection remains a close one. Apart from this fact, the

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[1] In the Chelonian *Cinixys homeana* there is a somewhat similar "tympanum," the vocal cords are wanting in the larynx, and the laryngeal muscles are reduced.

[2] Many differences are seen amongst the various avian groups as regards the syringeal muscles. In some, both tracheo-bronchial and sterno-tracheal muscles are wanting, while in others there may be as many as seven pairs. The syrinx is simpler and more primitive in the female than in the male.

[3] In some cases (*e.g.* Swan, Crane), the windpipe extends into the hollow keel of the sternum, where it becomes more or less coiled, and then again passes out close to its point of entrance and enters the body-cavity. In certain representatives of the Sturnidæ it extends between the skin and the muscles of the thorax, and there gives rise to numerous spiral coils.

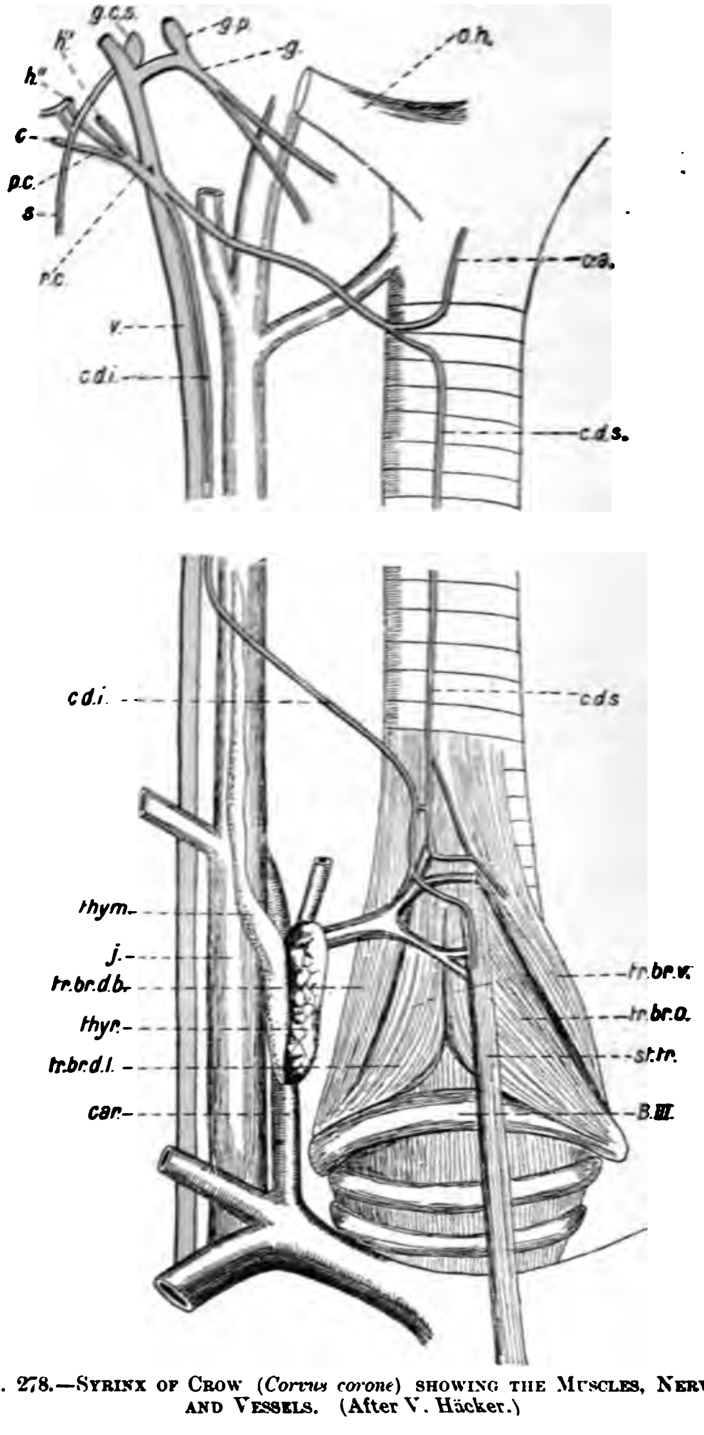

FIG. 278.—SYRINX OF CROW (*Corvus corone*) SHOWING THE MUSCLES, NERVES, AND VESSELS. (After V. Häcker.)

B.III, 3rd bronchial ring; *car*, carotid artery; *j*, jugular vein; *o.h*, hyoid (cut through): *thym*, thymus; *thyr*, thyroid.

Muscles and their insertions:—*st.tr*, sterno-trachealis; *tr.br.d.b*, trach.-bronch.-dorsalis brevis (membrana tympaniformis interna); *tr.br.d.l*, trach.-bronch.-dorsalis longus (dorsal end of *B.II*); *tr.br.o*, trach.-bronch.-obliquus (ventral end of *B.III*); *tr.br.v*, trach.-bronch.-ventralis (ventral end of *B.II* and pessulus).

Nerves:—*c*, 1st cervical; *c.a*, cervicalis ascendens; *c.d.i*, *c.d.s*, cervicalis descendens inferior et superior; *g*, glossopharyngeal; *g.c.s*, anterior (superior) cervical ganglion; *g.p*, petrosal ganglion (nearer to *g.c.s* than shown on figure); *h'* and *h"*, 1st and 2nd root of hypoglossal; *p.c*, cervical plexus; *r.c*, cervicalis; *s*, cervical sympathetic; *v*, vagus.

larynx of Monotremes, and especially of Echidna, exhibits a much more primitive condition than that of other Mammals. In these, the thyroid is unpaired, its two halves uniting ventrally, though still showing traces of its primary paired nature. This shield-shaped thyroid becomes separated from the hyoid, and surrounds the lateral and ventral regions of the larynx, overlapping the cricoid above,[1] and serving as a point of origin and insertion for important intrinsic and extrinsic muscles.

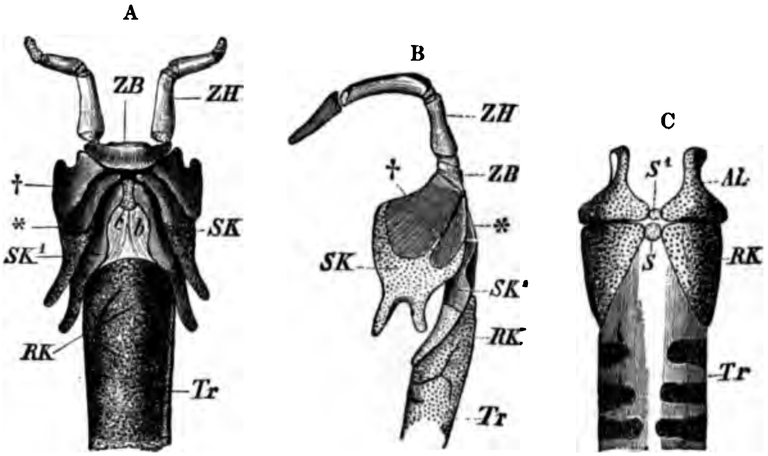

FIG. 279.—LARYNX OF ECHIDNA. (A, ventral, B, lateral, and C, dorsal view.)

AL, arytenoids, with an intercalary piece, S^1; *RK*, cricoid, with a dorsal intercalary piece, *S*; *SK*, skeletal element which is partially subdivided into two portions ventro-laterally; of these the anterior (†) corresponds to the greater cornu of the hyoid of other Mammals (that is, to the 3rd visceral arch), and the posterior (*) gives rise to the anterior thyroid element (=4th visceral arch); *SK'*, the posterior thyroid element (=5th visceral arch), with a basal piece or copula (*c*); *Tr*, trachea; *ZB*, body of hyoid (=copula of 2nd and 3rd visceral arches): *ZH*, lesser cornu (=2nd visceral arch).

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[1] The cricoid may be complete or incomplete ventrally, and its dorsal portion usually forms a broad plate with which the arytenoids are articulated (Figs. 280 and 281). The latter, growing out dorsally, may each give rise to a distinct corniculate cartilage (cartilage of Santorini).

The vocal cords extend between the thyroid and the arytenoids, and the mucous membrane above them becomes evoluted laterally

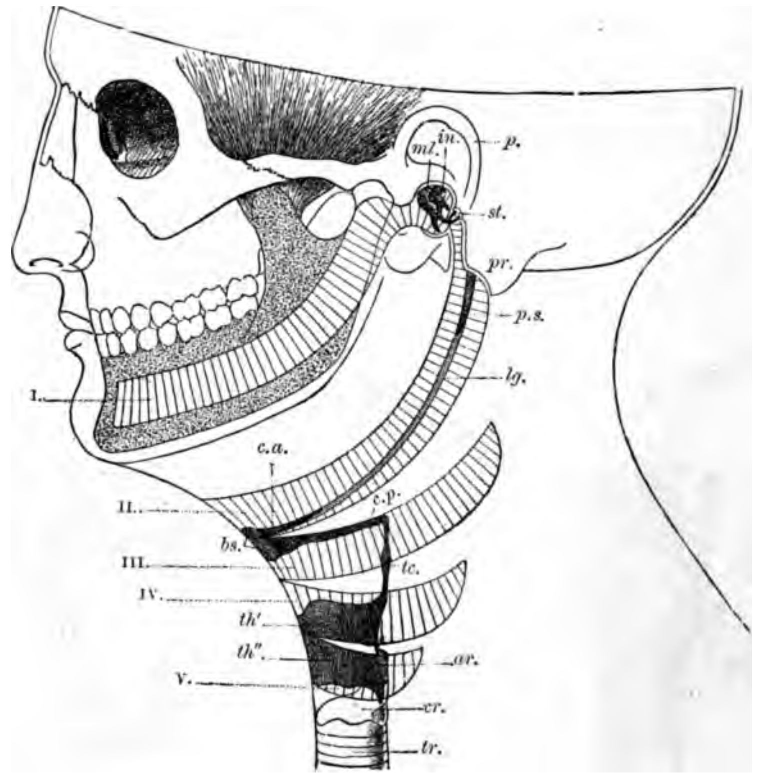

FIG. 280.—DIAGRAM TO ILLUSTRATE THE METAMORPHOSIS DURING DEVELOPMENT OF THE FIRST TO FIFTH VISCERAL SKELETAL ARCHES (I—V) IN MAN.

From the proximal end of the first arch (Meckel's cartilage) arise two of the auditory ossicles, the malleus and incus (*ml* and *in*). *p*, pinna; *pr*, mastoid process of skull.

From the second arch (hyoid) arise proximally the styloid process (*p.s*), distally the anterior (lesser) cornu of the hyoid (*c.a*) and a portion of the basi-hyoid (*b.s*). By far the greater portion of this arch becomes the stylo-hyoid ligament (*l.g*). [Concerning the stapes (*st*) cf. p. 134.]

The third (first branchial) arch gives rise to the greater part of the body (*b.s*) of the hyoid, and the posterior or greater cornu of the hyoid (*c.p*).

The fourth (second branchial) arch gives rise to the anterior (upper), and the fifth (third branchial) to the posterior (lower) segment of the thyroid cartilage (*th'*, *th''*). The arytenoid cartilage (*ar*) is probably a derivative of the fifth arch. *cr*, cricoid cartilage; *tc*, cartilago triticea, connecting the hyoid and thyroid; *tr*, trachea.

to form the laryngeal pouches, one (more rarely both) of which may undergo special development and in Anthropoids may reach such a large size that it serves as a resonance cavity. In other Monkeys, a median pouch projects between the epiglottis and thyroid cartilage (or more rarely between the latter and the cricoid), and may come to lie partially within the body of the hyoid, which (*e.g.* in Mycetes, Fig. 281)[1] is swollen to form a large bony chamber. The folds of mucous membrane bounding the laryngeal pouches anteriorly are spoken of as false vocal cords; these are not present in all Mammals. True vocal cords may also be wanting, being replaced functionally by a ridge of the mucous membrane which is only slightly vibratory and may be temporarily strengthened by the contraction of the thyro-arytenoid muscle (*e.g.* Monotremes, Cetaceans, Monkeys).

The epiglottis, which consists mainly of elastic fibro-cartilage, has close relations to the soft palate, extending upwards from the anterior border of the thyroid cartilage in front of the glottis, which it covers when pressed backwards: it is often, when at rest, embraced more or less firmly by the soft palate in such a way that its distal end lies in the passage of the posterior nostrils (naso-pharyngeal chamber), so that respiration and feeding can go on independently of one another.[2]

An interesting adaptation for the method of lactation is seen in the larynx of Marsupial embryos, in which it and the epiglottis become greatly elongated and are firmly embraced by the soft palate, so that it cannot be moved from this position. Thus respiration can go on freely while the milk is pumped down the œsophagus on either side of the larynx by the action of the compressor mammæ muscle of the mother. In Cetacea (more particularly the Odontoceti), a similar arrangement occurs, and is here adapted for the aquatic life of the animal. In all Mammals a similar position of the larynx is seen in the embryo if not in the adult.

The length of the trachea is proportional to that of the neck: when the latter is short, the two bronchi may arise close behind the cricoid cartilage (Sirenia): except in Bradypus, in which it takes a peculiar course, it lies close to the ventral side of the gullet. The cartilaginous rings are usually incomplete dorsally, where their open ends are connected by a membrane enclosing smooth muscle-fibres.[3] In the bronchi, the rings are only exceptionally closed on the dorsal side, and are usually present for a considerable distance along the intrapulmonary bronchi.

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[1] Outgrowths from various parts of the laryngeal mucous membrane may occur in various Mammals (*e.g.* Cetacea, Ungulates).

[2] The phylogenetic history of the epiglottis is unknown. It was probably originally a paired structure, and the small cartilages of Wrisberg are apparently derived from it.

[3] In the Cetacea they are incomplete ventrally, and in certain Marsupials and Rodents, as well as in Phoca and Lemur, they form complete rings.

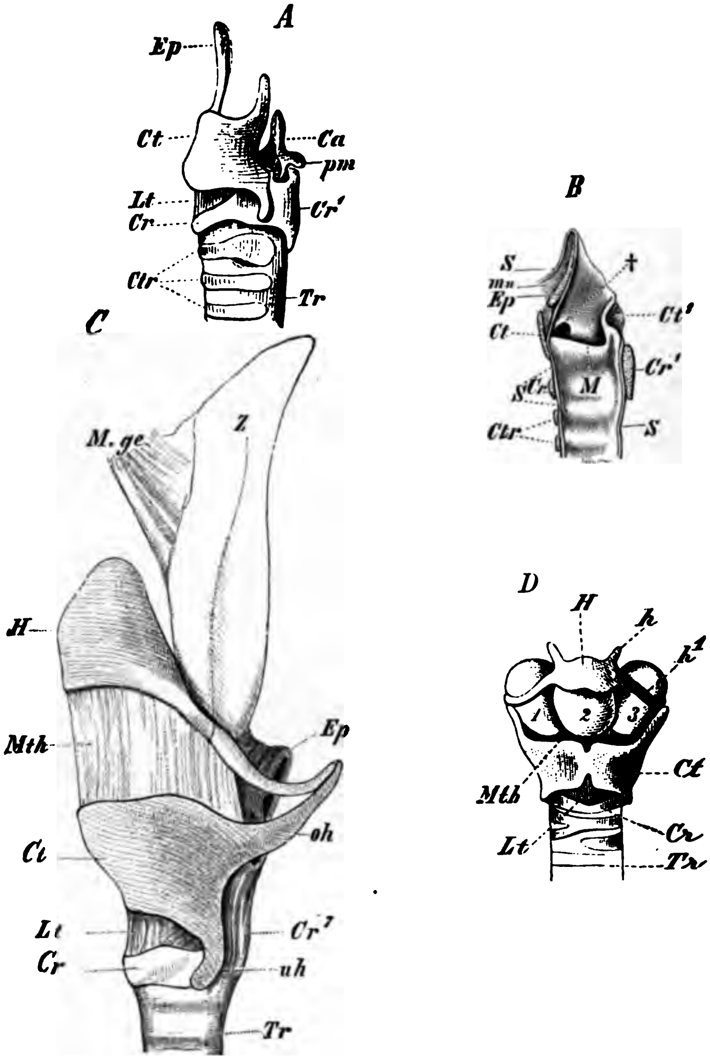

FIG. 281.—LARYNGES OF VARIOUS MAMMALS.

A, Deer, seen from the left side; B, Fox, longitudinal section; C, Howling Monkey (*Mycetes ursinus*), from the left side; D, Chimpanzee (*Simia troglodytes*), from the ventral side.

Ca, arytenoid cartilage; *Cr*, ventral, and *Cr*¹, dorsal plate of the cricoid; *Ct*, *Ct*¹, thyroid cartilage; *Ctr*, cartilaginous rings of the trachea; *Ep*, epiglottis; *H*, body of hyoid; *h*, lesser, *h*¹, greater cornua of the hyoid; *Lt*, crico-thyroid ligament; *M*, laryngeal pouch, which shows an enlargement at †; *M.ge*, genioglossus muscle; *Mth*, thyro-hyoid ligament; *mu*, submucous tissue with muscles; *oh*, *uh*, anterior and posterior cornua of the thyroid; *pm*, processus muscularis of the arytenoid; *S*, mucous membrane of the trachea and tongue; *Tr*, trachea; *Z*, tongue; *1*, *2*, *3*, resonance cavities.

The Lungs.

Dipnoans.—In Ceratodus the lung is a wide, unpaired sac without any trace of a dividing septum: in other Dipnoans it is distinctly paired (as in Polypterus, cf. p. 361) throughout the greater part of its length, the anterior unpaired portion being largely filled up by spongy trabeculæ.

The lung extends through the whole length of the body-cavity, and is covered by peritoneum on the ventral surface only; the lining mucous membrane forms bands and networks similar to those seen in the swim-bladder of many Fishes (*e.g.* Lepidosteus, Fig. 267), and smooth muscles are abundant.

Amphibians.—The lungs of Proteus and Necturus (Fig. 282), as well as those of the Newt (Triton), though paired throughout, remain at a lower stage than those of the Dipnoi, their internal surface being perfectly smooth, and having, therefore, a relatively much smaller superficial extent. They consist of two delicate, elongated sacs of unequal length and constricted in the middle; in Proteus they extend much further backwards than in Necturus. A difference in length between the two lungs is seen also in other Amphibia, such as Amphiuma and Siren, in which the two cylindrical lungs lie near together, close to the aorta. Their internal surface is raised into a network enclosing numerous smooth muscle-fibres and corresponding with the distribution of the blood-vessels, the meshes being much finer in Amphiuma, and still more so in Menopoma, than in Siren.

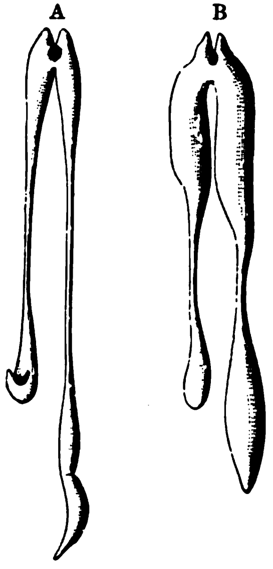

FIG. 282.—LUNGS OF PROTEUS (A) AND NECTURUS (B).

The communication with the pharynx is indicated by a black spot anteriorly.

With the further development of the blood-vessels, they gradually encircle the wall of the lung like the hoops of a barrel, so that septum-like structures arise, between which the thin pulmonary walls project in the form of rounded vesicular elevations (Fig. 283). Thus a beginning is made of a differentiation in the cavity of the lung into respiratory regions and air-passages (intra-pulmonary bronchi) such as is seen in higher forms.

In many other Urodela, as well as in the Anura and Gymnophiona, the muscular and elastic walls of the lung become still further complicated by the development of a respiratory network of trabeculæ, forming a system of alveoli lining the vesicles (Fig. 284). The lungs are, as a rule, equal in size; in form they are cylindrical in Salamanders, and elliptical in Anurans. In the long-bodied Gymnophiona the right lung alone is fully developed, the left being only a few millimetres long.

The mechanism of respiration is briefly as follows. The floor of the mouth (which is kept closed) is lowered, and thus air is inspired through the nostrils, which are then closed by a special mechanism, while the glottis is pressed forwards and opened. The floor of the mouth is next raised so that air is forced into the lungs. After a pause, the glottis and nostrils are opened, and thus expiration takes place. The mechanism is therefore that of a force-pump.

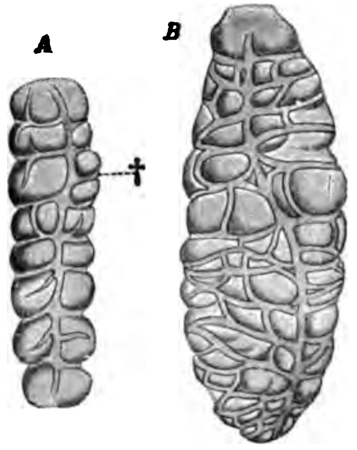

FIG. 283.—*A*, Lung of *Salamandra maculosa*, showing the regular arrangement of the blood-vessels extending between the individual vesicles; this regularity is slightly disturbed on the right side at †. *B*, Lung of *Rana temporaria*, in which the blood-vessels and vesicles have a more irregular arrangement. (After Fanny Moser.)

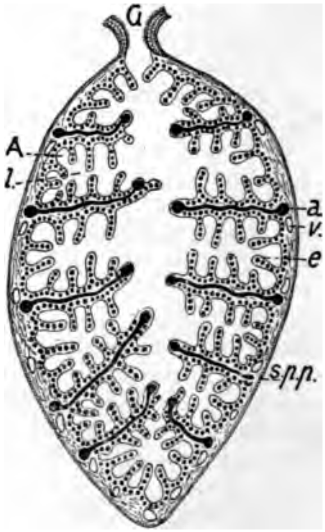

FIG. 284.—DIAGRAM OF A SIMPLE LOBULAR LUNG (FROG). (From Oppel, after Renault.)

A, alveoli; *a*, artery; *e*, epithelium of lung; *l*, vesicles lined by the alveoli; *G*, glottis; *s.p.p*, pleuroperitoneum; *v*, vein.

In many Salamanders (*e.g.* Salamandrina perspicillata, Typhlomolge, Amblystomatinæ, Desmognathinæ, Plethodontinæ) the lungs undergo a more or less complete degeneration, even though all traces of the gills disappear. The fact that the floor of the mouth is continually raised and lowered, as in other Amphibians which possess lungs, indicates that a bucco-pharyngeal respiration takes place in addition to the cutaneous respiration common to most Amphibians, in spite of the fact that the skin is especially vascular in these forms. The walls of the mouth, pharynx, and even œsophagus (Desmognathus fusca) are abundantly supplied with capillaries, which may even extend between the epithelial cells.

Reptiles.—In Reptiles, as in all other air-breathing Vertebrates, the form of the lungs is to a great extent regulated by that of the body. In the higher types, such as the Chelonia and Crocodilia, their structure is much more complicated than in Amphibia; this complication finds expression in a very considerable increase of the respiratory surface. With the exception of the thin-walled lungs of many Lizards, which retain a more primitive condition, more like that seen in the Frog except for the presence of transverse septa, we no longer meet with a large central cavity, but the organ becomes penetrated by a branched system of bronchi connected with a comparatively narrow central bronchus.

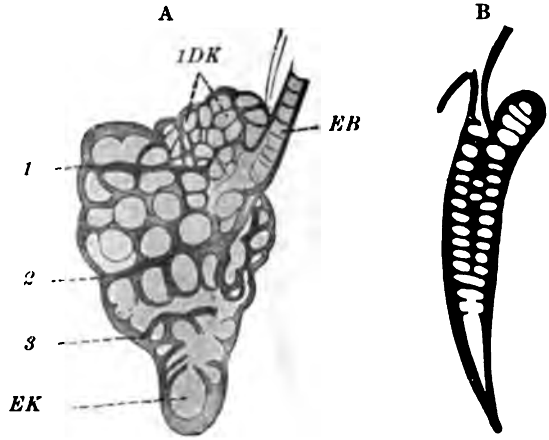

FIG. 285.—LUNG OF (A), *Emys lutaria* (1·6 MM. IN LENGTH), AND B, *Anguis fragilis*, BOTH RENDERED TRANSPARENT. (After Fanny Moser.)

In A are shown the three large transverse septa (1—3), which separate the lateral chambers, as well as the entrance of the extra-pulmonary bronchus (*EB*), the first anterior chamber (*1 DK*), and the posterior chamber (*EK*).

In the simplest condition the trachea opens into the lung by two bronchial apertures, but as the alveolisation of the lung increases, extrapulmonary portions of the bronchi are more marked: they are at first short, but gradually become longer, and each is continued into the corresponding lung as an intrapulmonary bronchus, which may be provided with cartilaginous rings along a considerable part of its course, and which is connected by means of numerous apertures with smaller secondary bronchi: these may again give rise to bronchi of a third order, and so on.

This high differentiation of the lung occurs even in certain Lizards, only its posterior end retaining a considerable lumen (Fig. 286), and is more marked in Chelonians and Crocodiles (Figs. 287 and 288). In Snakes, on the other hand, the central lumen (*i.e.* the main bronchus) remains more roomy, and, as in Amphisbænians, in correlation with the elongated form of the body, the right lung only is as a rule fully developed, the left remaining in a vestigial condition or even disappearing entirely.

The posterior end of the lung may be continued into a delicate finger-shaped hollow process, in which the alveoli are little marked or entirely wanting (*e.g.* certain Ascalabota, Iguanidæ, Varanidæ, and Testudinidæ). In Chameleons, in which, as in most other Lizards, only the anterior end of the lung is spongy, numerous thin-walled processes are given off from its ventral side, which are spindle-shaped, club-shaped, or lobular in form (Fig. 289). These processes seem to foreshadow a condition which reaches its highest development in Birds, but here have to do with the curious habit of inflating the body possessed by these animals.

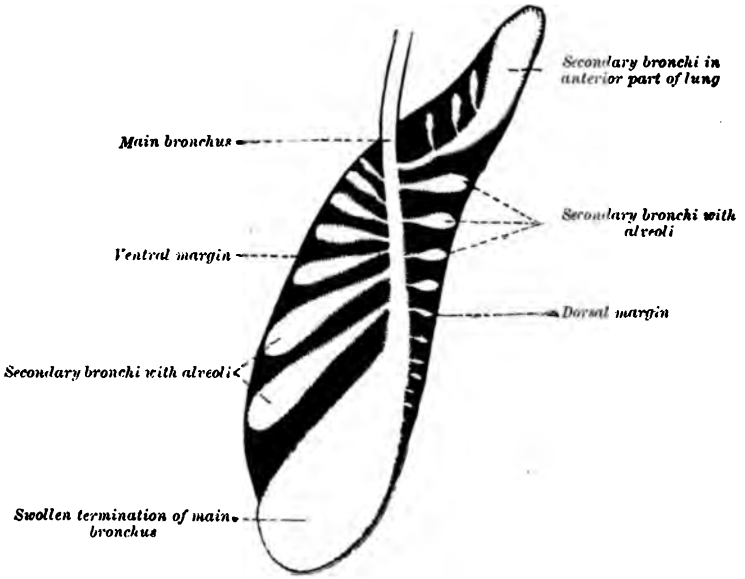
Secondary bronchi in anterior part of lung
Main bronchus
Secondary bronchi with alveoli
Ventral margin
Dorsal margin
Secondary bronchi with alveoli
Swollen termination of main bronchus

FIG. 286.—LUNG OF *Varanus varius*. (After A. Malani.)

The walls of the reptilian lung gradually undergo a considerable thickening owing to the increase in the amount of connective tissue, and the smooth muscles which are enclosed in them play an important part in the mechanism of respiration. A result of this thickening is that the branches of the intrapulmonary bronchus form comparatively narrow canals separated by mesodermic tissue.

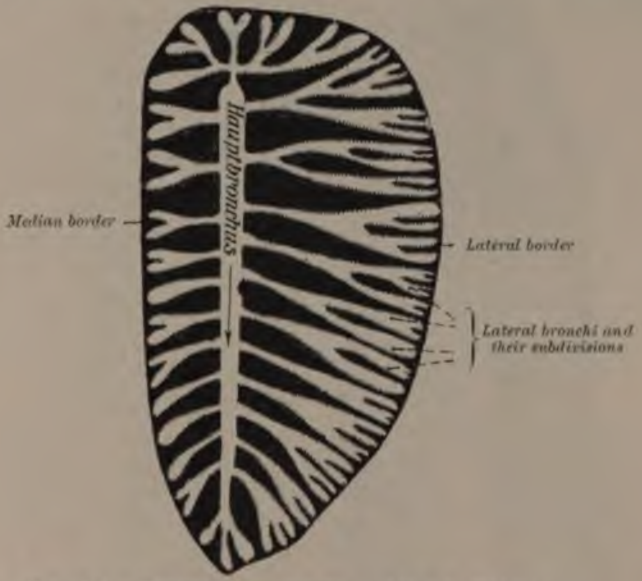

FIG. 287.—*Thalassochelys caretta.* (After A. Malani.)

Moreover, a distinction of the bronchi into portions serving merely for the passage of air and into respiratory portions becomes

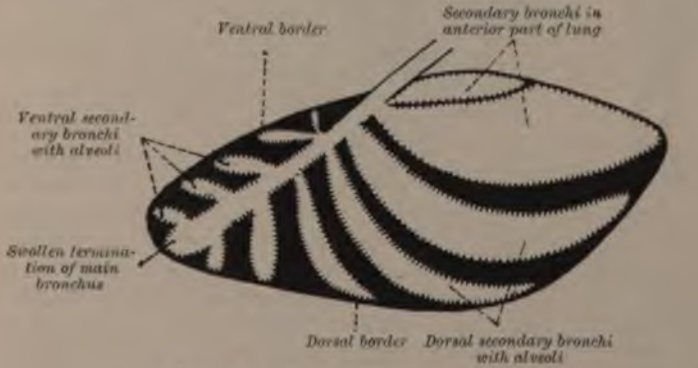
Ventral border
Secondary bronchi in anterior part of lung
Ventral secondary bronchi with alveoli
Swollen termination of main bronchus
Dorsal border
Dorsal secondary bronchi with alveoli

FIG. 288.—LUNG OF *Alligator mississipiensis.*

The bronchus enters the lung some distance from the anterior end. (After A. Malani.)

gradually more marked, and thus eventually leads to the condition seen in Birds and Mammals. Both ontogenetically and phylo-

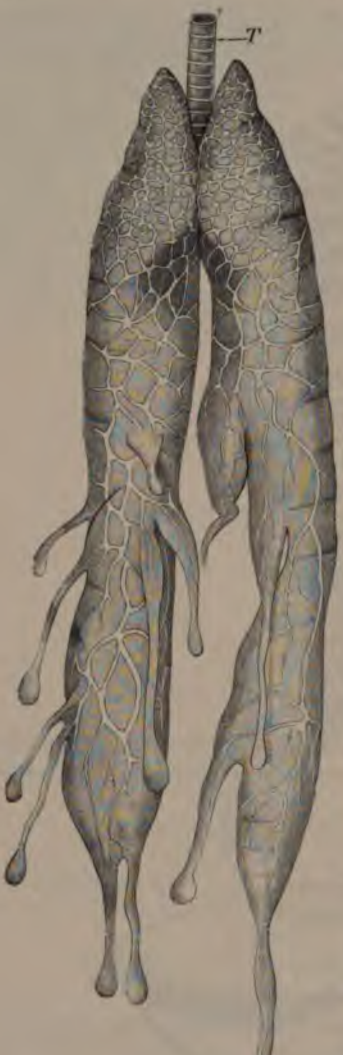

FIG. 289.—LUNGS OF *Chamæleo monachus*.
T, trachea.

genetically a process of centrifugal budding of the endodermic epithelium followed by a further development of the mesodermic portions gradually results in a complicated structure of the lung such as occurs in the higher forms.

Birds.—The respiratory apparatus of Birds presents so many remarkable peculiarities, both as regards the structure of the lungs and in the presence of *air-sacs*, that it must be considered in some detail. Physiologically, it reaches the highest degree of perfection amongst Vertebrates.

The comparatively small but highly vascular lungs (Figs. 290 and 291) are closely applied to the thoracic vertebræ and heads of the ribs, and are but slightly elastic and capable of very little distension. The lower surface of each lung is closely invested by a thin fibrous membrane, the *pulmonary aponeurosis*,[1] into which are inserted a variable number of muscular bands (*costo-pulmonary muscles*): these arise from the vertebral ribs, and are supplied by the intercostal nerves.

The main bronchus (mesobronchium) enters the lung at about the middle of its ventral surface, and gradually losing its cartilaginous rings, extends to the posterior end, giving off secondary bronchi. Of these, eight are ventral (entobronchia) and six to ten dorsal (ectobronchia), and the branches of small calibre which arise from them are perforated by numerous close-set apertures leading into small tubes—the so-called "lung-pipes" (parabronchia). These again, give off short, radially arranged bronchioli

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[1] The pulmonary aponeurosis, as well as the oblique septum, is often spoken of as a "diaphragm" (cf. p. 184).

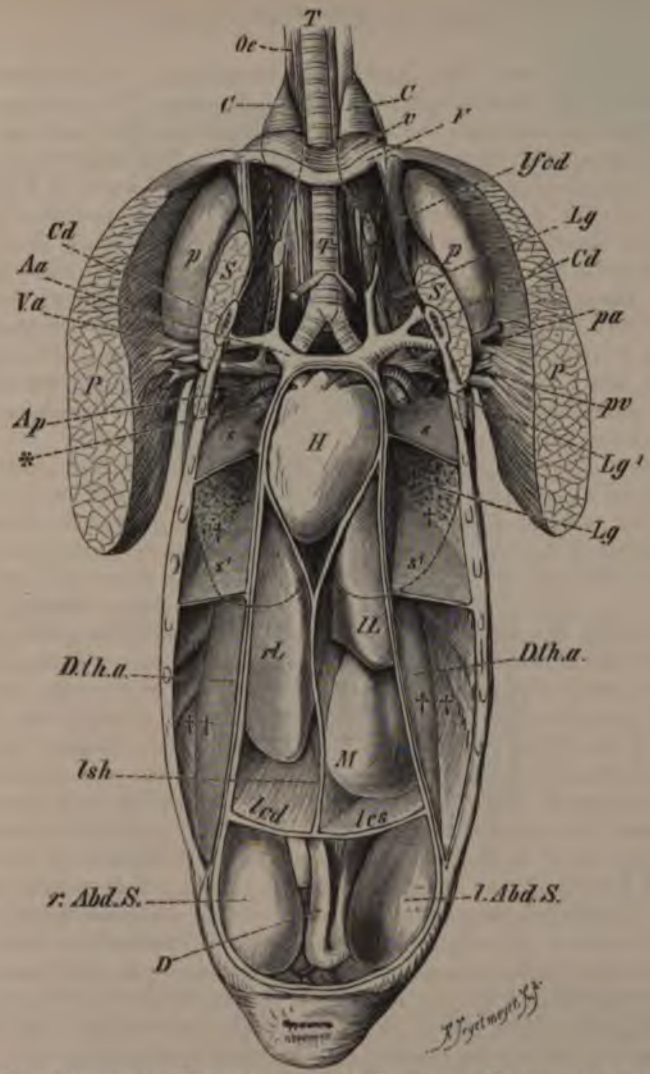

FIG. 290.—ABDOMINAL VISCERA AND AIR-SACS OF A DUCK AFTER THE REMOVAL OF THE VENTRAL BODY-WALL. (From a drawing by H. Strasser.)

Aa, *Va*, innominate artery and vein with their branches; *Ap*, pulmonary artery; *C*, *C*, cervical sacs; *Cd*, coracoid; *D*, intestine; *D.th.a*, oblique septum; *F*, furcula; *H*, heart, enclosed within the pericardium; *lfcd*, coraco-furcular ligament; *Lg*, Lg^1, lung; *lsh*, suspensory (falciform) ligament, and *lcd*, *lcs*, right and left coronary ligament of the liver; *P*, pectoralis major; *p*, axillary sac lying between the coracoid, scapula, and the anterior ribs, and communicating with the sub-bronchial air-sac; *pa*, *pv*, pectoral artery and vein; *r.Abd.S*, *l.Abd.S*, right and left abdominal (posterior) air-sac; *rL*,*lL*, right and left lobes of liver; *S*, subclavius muscle; *s*, *s*, partition walls between the anterior thoracic air-sacs and the unpaired sub-bronchial sac, lying in the anterior part of the body-cavity; s^1, s^1, partition walls between the anterior and posterior thoracic air-sacs; *T*, trachea; *v*, portion of anterior wall of the body-cavity; *, point of entrance of the bronchi into the lung; †, anterior thoracic air-sac; ††, posterior thoracic air-sac.

which divide into finer and finer branches ("air-capillaries") with which the blood-capillaries are interwoven. The delicate air-passages communicate with one another, so that none of the alveoli apparently end blindly (Fig. 294, A). The relative delicacy of the bronchial network is proportionate to the power of flight.

When the ventral body-wall of a Bird is removed, the heart, stomach, liver, and intestine are seen in the middle, and on either side of them is a tightly-stretched fascia, the *oblique septum*, which shuts them off from a paired lateral *sub-pulmonary chamber* (Fig. 290). Other chambers are situated in the anterior thoracic region, ventral to the lungs. Others, again, are seen in the region of the heart and in the posterior part of the abdominal cavity. These chambers are occupied by the *air-sacs* with which certain of the bronchi communicate.

The most posterior chamber on either side encloses an *abdominal* (*posterior*) air-sac (Fig. 290). In Apteryx, this is completely closed in by the oblique septum, but in other Birds it gives rise to a large, distensible diverticulum which extends backwards ventrally to the kidney, amongst the viscera. In front of this there are two air-sacs lying above and externally to the oblique septum, and constituting the main part of the sub-pulmonary chamber; these may be called the *anterior* and *posterior thoracic* sacs. A transverse dividing-wall separates these, at the level of the cœliac artery, and a second septum shuts off the anterior thoracic sac from another one lying in front of it. The posterior thoracic air-sac presents the simplest and most constant relations, and never communicates with any of the neighbouring chambers, as is often the case with the anterior thoracic sac. A pair of *cervical* air-sacs lies on either side of the œsophagus above each bronchus, anterior to the hilum of the lung, and below this a *sub-bronchial* sac is situated, which is separated behind from the anterior thoracic sac by the septum already referred to. This sac is usually unpaired, that of either side fusing with its fellow to form an *interclavicular* chamber, bounded by the furcula[1]; it communicates with neighbouring air-cavities which lie between the pericardium and sternum and in the axilla, outside the body-cavity (*axillary sac*).

The main bronchus (*mesobronchium*) as a rule opens directly into the abdominal air-sac (Fig. 291). From it a large lateral bronchus is given off, which opens into the posterior thoracic sac by one or two apertures. The first entobronchium radiates out anteriorly to the hilum of the lung, and one of its branches opens into the cervical sac. Almost without exception, a large aperture or ostium is present on the wall of the third entobronchium, communicating with the anterior thoracic air-sac. A branch of the second entobronchium opens externally to the hilum of the lung into the sub-bronchial sac.

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[1] In some Birds (*e.g.* Rhea, Vulture, Adjutant) a median septum is present separating the two sub-bronchial sacs.

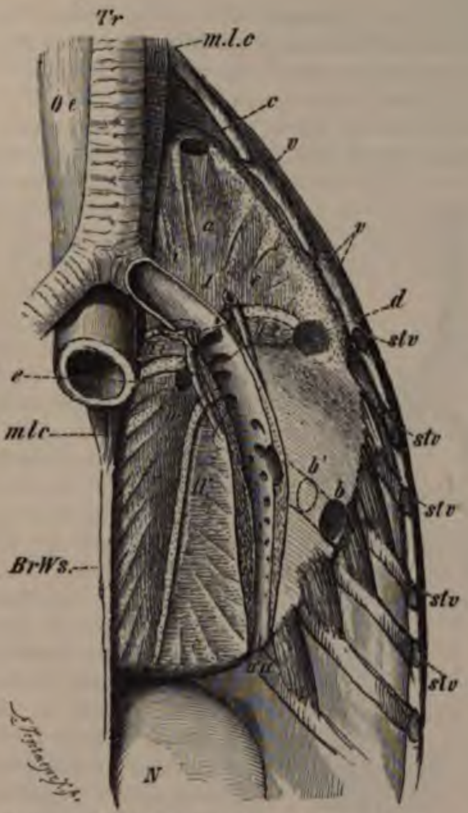

FIG. 291.—LEFT LUNG OF THE DUCK, *in situ*. (From a drawing by H. Strasser.) The main bronchus is cut open; internally to it lies the pulmonary vein, and externally the pulmonary artery.

au, opening of the main bronchus into the abdominal sac; *b*, opening of the outer lateral branch of the mesobronchium into the posterior thoracic air-sac; b^1, second ostium of the latter, more towards the middle line (present in Passeres); *Br. Ws*, thoracic vertebræ; *I*, first entobronchium, and *c*, its ostium communicating with the cervical air-sac; *i*, *a*, *e*, its internal, anterior, and external branches; *IIe*, *IIi*, internal and external branch of the second entobronchium: the end of *IIe* opens into the sub-bronchial sac at *d*; *III*, third entobronchium, with the aperture for the anterior thoracic air-sac; *IV*, fourth entobronchium; *m.l.c*, longus colli muscle; *N*, kidney; *Oe*, œsophagus; *stv*, *stv*, sections of ribs which are connected with the sternum; *Tr*, trachea; *v*, *v*, ends of free vertebral ribs. The boundary of the pulmonary aponeurosis is seen along the outer edge of the lung, and the costopulmonary muscles are shown extending from it to the ribs.

The air-sacs arise from the embryonic pulmonary vesicles as delicate-walled hollow processes, lined by pavement epithelium: these grow rapidly, and soon exceed the lung proper in size, extending amongst the viscera. Moreover, they are not confined to the body-cavity, but in numerous places extend beyond it, passing between the muscles, beneath the skin, and even into most of the bones. The latter are thus rendered *pneumatic*, and consequently the buoyancy of the body is increased. The pneumaticity of the bones is not, however, an essential peculiarity connected with flight, for in many Birds which are extremely good fliers (*e.g.* Larus, Sterna) the bones are hardly if at all pneumatic, while in the cursorial Ratitæ, on the other hand, they are markedly so.[1]

The air-sacs, though not serving to increase the actual respiratory surface,[2] must be looked upon as an integral part of the respiratory apparatus: by their means, a greater quantity of air can rapidly pass in and out through the lungs when the body-cavity is expanded and contracted during inspiration and expiration respectively, especially through the larger bronchi; consequently there is less need for the expansion of the lung-parenchyma. Moreover, as part of the inspired air passes directly into the air-sacs and their prolongations, the absorption of oxygen can take place during expiration as well as inspiration. The aëration of the blood is thus very perfect and its temperature correspondingly high.

Rhythmical respiratory movements take place when the Bird is at rest, the sternum being alternately raised and lowered. But during flight, when the weight of the body is supported by the wings, the sternum, as well as the coracoid and ribs, are relatively immovable, and inspiration and expiration are effected by the raising and lowering of the wings, which may take place from three to thirteen times in the

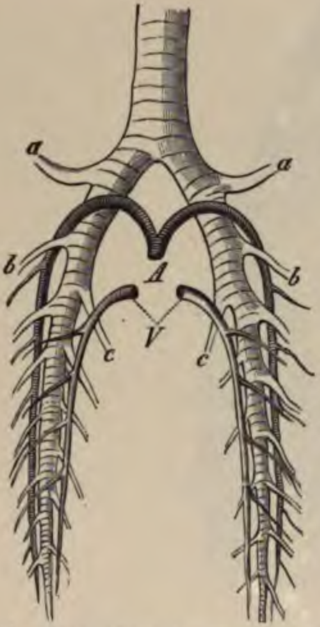

FIG. 292.—DIAGRAM OF THE ARRANGEMENT OF THE BRONCHI IN MAMMALS. From the ventral side.

A, pulmonary artery; *a*, *a*, "eparterial" bronchus of either side; *b*, series of ventral, and *c*, of dorsal "hyparterial" bronchi; *V*, pulmonary vein.

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[1] The bones of Archæopteryx were solid, and those of the recently extinct Moa of New Zealand were much less pneumatic than in existing Ratitæ.

Pneumaticity of the bones is not a special peculiarity of Birds; it occurred amongst the gigantic fossil Dinosaurians, and the skull of Crocodiles is also pneumatic. Amongst Mammals, frontal, maxillary, and sphenoidal sinuses are present in Anthropoids, Ungulates, Elephants, and Marsupials for instance: and all these communicate with one another, and also with the tympanic cavity. They are in many cases developed in order to give a greater surface for the attachment of muscles, and also to effect a saving of material and a lightening of the skull.

[2] The walls of the air-sacs are supplied with blood by small nutrient arteries arising from the aorta, the veins communicating with the postcaval.

second. Thus during flight the air passes in and out without any special respiratory movements being made, and the bird can travel rapidly and continuously through the air without getting out of breath.

A further importance of the air-sacs consists in the resulting enlargement of the anterior part of the body surrounded by the pectoral arch. An extended development of the skeleton can thus take place, giving an increase of surface for muscular attachment without any considerable increase in weight. Everything, in fact, combines to establish an organ of flight with a large wing-surface and increased muscular power.

Mammals.—Though not directly derived from the reptilian type of lung, a certain parallelism can be recognised between the lung of Reptiles and that of the Echidna as regards, for instance, the presence of large air-spaces; but the resemblance here is probably only of a secondary nature.

The main bronchus extends throughout the length of the lung and gives off a double row of secondary bronchi on its dorsal and ventral aspects respectively, the components of the ventral system being larger than those of the dorsal.[1]

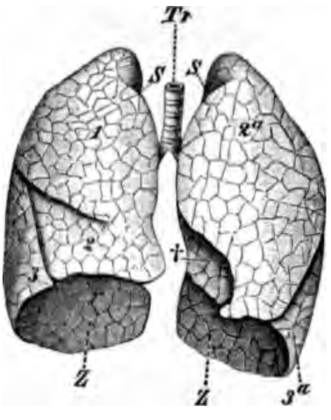

FIG. 293.—LUNG OF MAN. From the ventral side.

S, sulcus for the subclavian artery; *Tr*, trachea; *Z*, base of lung; †, incisura cordis; 1, 2, 3, lobes of the right, and 2*a*, 3*a*, of the left lung.

The morphological importance of the lobes into which the lungs are usually more or less divided (Fig. 293) is secondary to that of the branching of the bronchi, and does not essentially affect the latter: the furrows between the lobes frequently disappear to a greater or less extent. The right lung possesses in many cases an accessory lobe anteriorly, and another posteriorly, the former in connection with an apical bronchus and the latter ("azygos lobe") with an accessory bronchus arising ventrally from the main bronchus, and this accessory bronchus may be present even if the azygos lobe is undifferentiated.

The cartilages of the bronchi become more and more sparse and finally disappear as the latter divide up into finer and finer branches. The ultimate bronchioles open into small terminal vesicles, the *sacculi alveolares* or "*infundibula*" (Fig. 294, B), which are surrounded by a close network of capillaries, and the walls of which are swollen to form numerous alveoli, thus causing a considerable increase in the respiratory surface of the vesicles, the size of which varies in different Mammals.

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[1] The most anterior of the bronchi may arise from the main bronchus—or even from the trachea—anteriorly to the point at which the pulmonary artery crosses the main bronchus, and thus has been distinguished as the "eparterial bronchus" from the others, or "hyparterial bronchi," which arise posteriorly to this point (Fig. 292). As a general rule, an "eparterial bronchus" is present on the right side only, and as the nature and meaning of this asymmetry are not clear, it is better to speak of the anterior secondary bronchi, whether "eparterial" or "hyparterial," merely as *apical bronchi.*

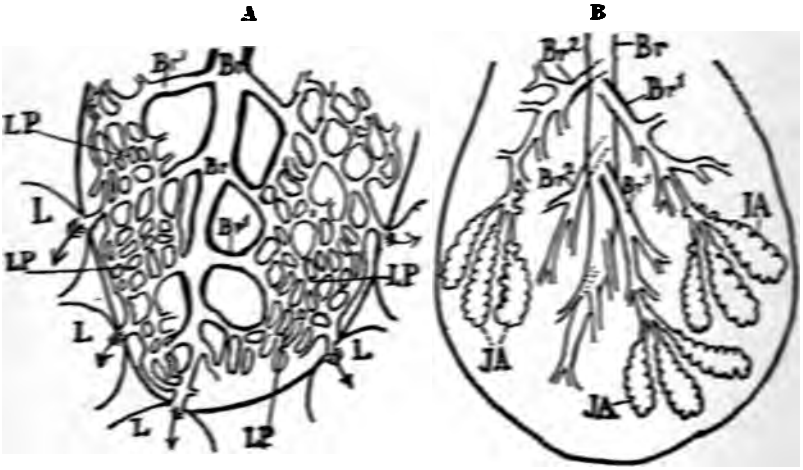

Fig. 294.—Diagram of the Structure of the Lung in A, Birds, and B, Mammals. (The whole of the lung is not represented.)

A. *Br*, main bronchus; *Br*¹, secondary bronchi; *LP*, "lung-pipes" (parabronchia). The arrows indicate the ostia of the air-sacs (*L*).
B. *Br*, main bronchus; *Br*¹, ventral, and *Br*², dorsal secondary bronchi; *JA*, sacculi alveolares ("infundibula"), only a few of which are indicated.

CŒLOME.

Serous Membranes.—In the Anamnia, the serous membrane (*pleuro-peritoneum*) lining the cœlome is continuous throughout (cf. p. 184 and Fig. 101) except that the heart is enclosed in a special pericardial chamber usually completely shut off from the rest of the cœlome[1] and enclosed by the *pericardial membrane*. In Reptiles an indication of a further subdivision is seen: thus in Crocodiles and Chelonians a chamber in which the lungs are situated is shut off from the rest of the abdominal cavity. In Birds, this subdivision is still more marked, and finally in Mammals, on account of the development of the diaphragm, the pleuroperitoneal cavity is divided into two main sections, an anterior *pleural* and a posterior *peritoneal* chamber.

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[1] In Elasmobranchs it communicates with the general body-cavity by pericardio-peritoneal canals.

In each of these three serous membranes (pericardial, pleural, and peritoneal), a parietal and a visceral layer can be distinguished, the former lining the outer wall of the chamber in question, and the latter being involuted so as to invest closely and to suspend its contained organ or organs.[1]

Towards the middle line, the parietal layer of the pleura of either side is reflected so as to form a septum between the right and left thoracic cavities. This septum is called the *mediastinum*, and the space between its two layers the *mediastinal space:* through this, the aorta, œsophagus, and postcaval vein run, and in the region of the heart the mediastinum is reflected over the parietal layer of the pericardium. There is a lymphatic fluid between the two layers of all these membranes, which renders the movements of the contained organs smooth and easy.

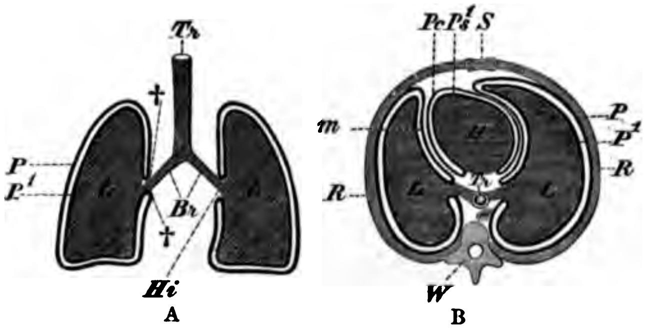

FIG. 295.—DIAGRAM OF THE PLEURAL AND PERICARDIAL CAVITIES OF MAMMALS, BASED ON THE RELATIONS IN THESE PARTS IN MAN. (A, horizontal section; B, transverse section.)

Br, bronchi; *H*, heart; *m*, mediastinum; *L*, lung; *P*, parietal, and P^1, visceral layer of the pleura; *Pc*, Ps^1, parietal and visceral layers of the pericardium; *R*, ribs (wall of thorax); *S*, sternum; *Tr*, trachea; *W*, vertebral column; ††, points at which the parietal and visceral layers of the pleura pass into one another at the hilum pulmonalis (*Hi*).

Abdominal pores.—By the term abdominal pore is understood a perforation—usually paired—of the posterior end of the wall of the peritoneal cavity which puts the cœlome into direct communication with the exterior.

In Cyclostomes a pair of pores opens into the urinogenital sinus, serving to conduct the generative products to the exterior: they probably do not correspond to the abdominal pores of other forms, which normally do not have this function, and are better described as *genital pores*, comparable to the like-named pores of Teleosts (cf. under Generative Organs).

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[1] In connection with the suspensory mesenteric structures in the peritoneal cavity, mention must be made of the *omental folds* extending between the abdominal viscera.

Apart from the indirect connection of the cœlome with the exterior by means of the oviducts in the female, such as exists in most Vertebrates, other connections are seen, for example, in both male and female Elasmobranchs. These are either indirect, through the nephostomes of the kidney (*q.v.*), or direct, through the abdominal pores: in some cases, both these means of communication with the exterior exist in the same Elasmobranch, but this is never the case in other Anamnia, so that they appear to be to a great extent mutually exclusive.

In the Elasmobranchii the abdominal pores are usually paired and are situated posteriorly to the cloaca (Figs. 296 and 297), and may be enclosed within its lips. They are wanting in the Notidanidæ, Cestracionidæ, and Rhinidæ, and are not constantly present in the Scylliidæ and others, even in individuals of the same species, and they may only appear at sexual maturity. In Ganoids, they open between the urinogenital aperture and anus, but are apparently wanting in Amia when sexually mature. Amongst Teleosts, they are said to be present only in the Salmonidæ and Mormyridæ, right and left of the anus; but even in these, the pore of one or of both sides may be absent. In Ceratodus the abdominal pores are paired, and open behind the

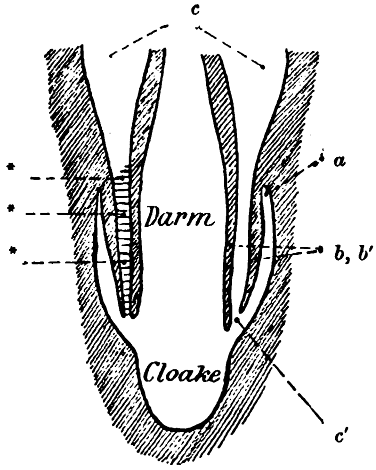

Fig. 296.—Diagrammatic Horizontal Section through the Cloacal Region of a Plagiostome. (After E. J. Bles.)

a, blind ectodermal invagination (cloacal pouch); *b*, b^1, cloacal papilla; *c*, peritoneal cavity, which opens by the abdominal pore at c^1; *Cloake*, cloaca; *Darm*, rectum; ***, points along the transversely striped section of the cloacal papilla at which the abdominal pore may break through, in which case the distal part of the papilla is solid (Raja).

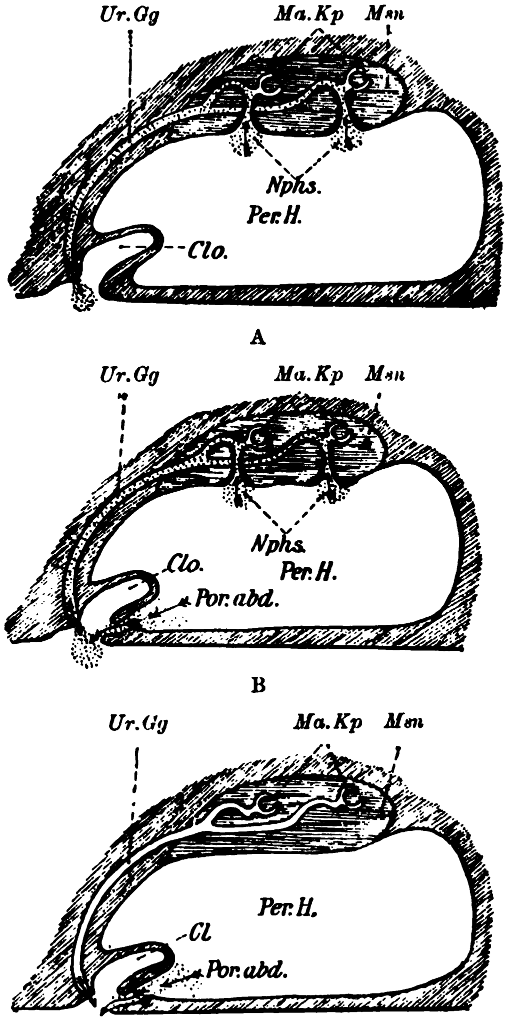

Fig. 297.—Diagrams illustrating the Three Possible Ways in which the Peritoneal Cavity may Communicate with the Exterior in Fishes. (After E. J. Bles).

A. Connection by means of nephostomes (*Nphs*) only (Cestracion, Rhina, certain other Elasmobranchs before sexual maturity, larval Amia).

B. Connection by means of nephostomes (*Nphs*) and abdominal pores (*Por.abd*) (certain adult Scylliidæ and Spinacidæ).

C. Connection by means of abdominal pores (*Por.abd*) only (Carchariidæ, Lamnidæ, Batoidei, Holocephali, adult Ganoids, certain Dipnoi and Salmonidæ, Mormyridæ).

Cl, *Clo*, cloaca, *Ma.Kp*, Malpighian capsules of the mesonephros (*Msn*); *Per.H*, peritoneal cavity; *Ur.Gg*, mesonephric duct.

cloaca, while in Protopterus a single, apparently blind, canal is present on the same side of the ventral fin as the vent, sometimes to the right and sometimes to the left of the middle line, either within or without the sphincter of the cloaca.[1]

Abdominal pores are not known to occur in Amphibians, Birds, and Mammals, but amongst Reptiles they are perhaps represented by the *peritoneal canals* of the Chelonia and Crocodilia, which in the former are in close relation with the penis or clitoris, and usually end blindly, while in the latter they open into the cloaca.

The abdominal pores may possibly correspond to the remains of segmental ducts. At any rate, they and the nephostomes, whichever may be the older phylogenetically, come under the same physiological category, inasmuch as both might serve to remove the products of regressive metamorphosis from the cœlome, which to a large extent represents an excretory organ (cf. Fig. 297).

[1] Abdominal pores are apparently wanting in Lepidosiren.

H. ORGANS OF CIRCULATION.

(VASCULAR SYSTEM.)

In Amphioxus, the vessels are of a simpler type than in the Craniata, and to a certain extent retain characters only seen in the embryos of the latter. There is no heart, and the circulation of the blood is effected by the peristaltic contraction from behind forwards of the ventral blood-vessel (ventral aorta).

In the Craniata the vascular system, which arises from the mesoderm, consists of a hollow central muscular organ, the **heart,** which is connected with a series of closed tubes, the **blood-vessels,** containing a coloured fluid, the **blood**: there is also another system of vessels containing a colourless fluid, the **lymph**, which, however, besides permeating all the tissues, is present in various spaces or *sinuses* in the body as well as in the **lymph-vessels**. The lymphatic system is therefore not completely closed, the vessels communicating with the sinuses on the one hand, and with the blood-vessels on the other. The lymph-vessels coming from the intestine are known as *lacteals.*

The blood, which serves to carry the absorbed food and oxygen to, and the waste products from, all parts of the body, is kept in constant circulation through the vessels by the rhythmic contraction of the heart, which acts both as a force-pump and a suction-pump.

All the blood-vessels which bring back the blood to the heart are known as **veins**, while those which carry it from the heart are called **arteries**: the latter usually contain oxygenated blood of a bright red colour, the former impure, darker blood, rich in carbon dioxide and other products of destructive metabolism; but this is by no means always the case. Many of the veins, and also of the lymph-vessels, are provided with *valves,* which are adapted to prevent the reflux of the blood: they usually have the form of semilunar folds of the internal coat, and are so arranged that two are placed opposite to one another. The arteries (and also certain of the veins) divide up into smaller and smaller branches, eventually giving rise to microscopic tubes called **capillaries**, the walls of which consist of a single layer of epithelial cells, surrounded by contractile structures analogous to the smooth muscle-fibres of the larger vessels and consisting of branched muscle-cells which are under the control of the nervous system: the capillaries again unite to form the factors of the veins. The walls both of veins and arteries consist, in addition to the epithelium, of connective and elastic tissue and of unstriated muscular fibres, and are much thicker in the case of the arteries than in that of the veins, in some of which the muscular elements may be altogether wanting.

Both blood and lymph consist of a colourless fluid, the *plasma*, in which float numerous *cells* or *corpuscles*. The *blood-corpuscles* are of two kinds—colourless, nucleated, amœboid cells, known as *white* or *colourless corpuscles* or *leucocytes*, and far more numerous *red blood-corpuscles* or *erythrocytes*.[1] The colour of these is due to *hæmoglobin*, which readily enters into loose chemical combination with oxygen, and they are the specific respiratory cells. They have no longer, however, the characteristic structure of protoplasm, and are always surrounded by a membrane. The lymph contains leucocytes only; these are similar to those of the blood, and are sometimes also spoken of as *phagocytes*.[2]

The nuclei of the red corpuscles persist, and the whole cell is biconvex, in all Vertebrates below Mammals; and, even in these nucleated red cells may be seen in the marrow of the bones (in which more especially they are formed throughout life), in the blood of the spleen, and often in that of the portal vein: in all other parts of the body of Mammals they lose their nuclei. In all Mammals, except the Camelidæ, the red corpuscles are seen to have the form of circular, biconcave discs;[3] in the last-mentioned family and in all other Vertebrates except Cyclostomes they are oval. They are largest in certain Urodeles, being in Amphiuma as much as 75μ in their longest diameter; then come, in order, other Urodeles and Dipnoans, Reptiles, Anurans, Fishes, Birds, and Mammals, in the last-mentioned of which they are the smallest, varying in different families from $2{\cdot}5\mu$ (Tragulidæ) to 10μ.

The heart is enclosed within a serous membrane, the *pericardium* (Fig. 295), which, as already mentioned, consists of parietal and visceral layers. In most Anamnia and in early embryos of higher forms it is situated close to the head, but on the differentiation of a neck, comes to lie relatively further back. It arises either as a single (Cyclostomi, Elasmobranchii, Ganoidei, Amphibia) or as a paired (Teleostei, Sauropsida, Mammalia) tubular cavity in the splanchnic layer of the mesoderm along the ventral region of the throat, close behind the gill-clefts, and the part of the cœlome around it gives rise to the pericardial cavity. Its wall becomes differentiated into three layers, an outer serous (*pericardium*), a middle muscular (*myocardium*), and an inner epithelial (*endocardium*).[1] In this respect it essentially corresponds with the larger vessels, in the walls of which, as already mentioned, three layers can also be distinguished; but in the heart the muscular fibres are striated, and the boundaries between the cells of which they are primarily composed may disappear, so that a syncytium results.

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[1] In Amphioxus the blood contains no formed elements.

[2] In addition to the leucocytes and erythrocytes, a third kind of corpuscle occurs in the blood: these structures are known as *blood-plates* or *thrombocytes*. Each has the form of a minute, flat disc, is colourless and amœboid, and consists of nucleated protoplasm. It is very possible that they are derivatives of the red and white corpuscles. In coagulation of the blood they undergo characteristic changes.

[3] They are said to be primarily cup-shaped.

By a study of its development we thus see that the heart corresponds essentially to a strongly-developed blood-vessel, which later becomes complicated by the formation of various folds and swellings. The embryonic tubular heart, which contracts peristaltically, undergoes a division into two chambers, an *atrium* or *auricle*, and a *ventricle*, between which valvular structures arise from the endocardial layer: these only allow the blood to flow in a definite direction on the contraction of the walls of the heart, viz., from the atrium to the ventricle, and any backward flow is thus prevented (Fig. 298).

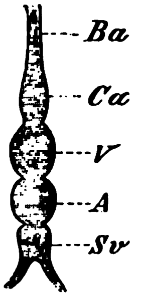

FIG. 298.—DIAGRAM SHOWING THE PRIMITIVE RELATIONS OF THE DIFFERENT CHAMBERS OF THE HEART.

A, atrium or auricle; *Ba*, bulbus and *Ca* conus arteriosus (together constituting the embryonic truncus arteriosus); *Sv*, sinus venosus, into which the veins from the body open: *V*, ventricle.

The atrium, into which the blood enters, represents primitively the venous portion of the heart, the ventricle, from which the blood flows out, corresponding to the arterial portion. The venous end further becomes differentiated to form another chamber, the ***sinus venosus***, which opens into the atrium by a narrow aperture provided with two valves; while the arterial end gives rise distally to a ***truncus arteriosus***; the proximal muscular end of this (*conus arteriosus* or *pylangium*) is provided with more or less numerous valves arranged in longitudinal rows, and its distal end (*bulbus arteriosus* or *synangium*) is continued forwards into the arterial vessel (***ventral aorta***).

These four chambers of the heart now contract rhythmically in the following order: sinus venosus, atrium, ventricle, conus arteriosus. The bulbus, which may be more or less swollen and corresponds to the base of the ventral aorta, contains no striated muscular fibres.

The ventral aorta gives off right and left a series of symmetrical *afferent branchial arteries* (Figs. 299–301, 320 and 321), each of which runs between two consecutive gill-clefts, branches out into capillaries in the gills, when present, and then becomes continuous with a corresponding *efferent branchial artery*. After the first pair of these has given off branches to the head (*carotids*), they all unite above the clefts, usually forming a longitudinal trunk on either side: these constitute the right and left roots of the *dorsal aorta*, which

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[1] The epithelial lining of the heart is said by some embryologists to be derived from the endoderm, by others from mesenchymatous cells.

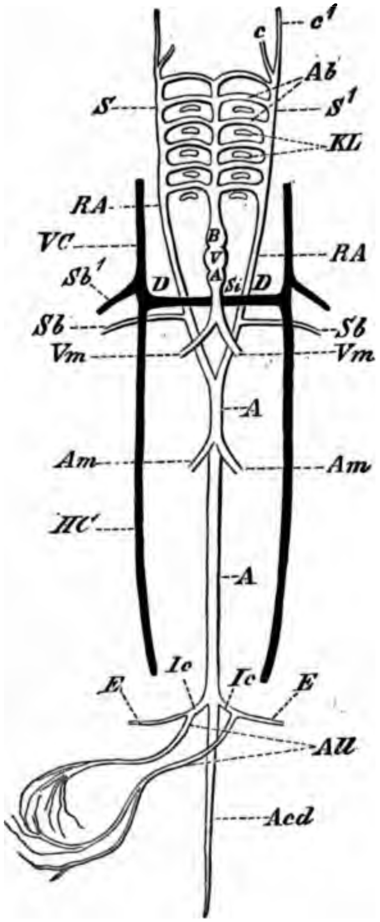

FIG. 299.—DIAGRAM OF THE EMBRYONIC VASCULAR SYSTEM FROM THE VENTRAL SIDE. (The portal systems are not shown.)

A, atrium ; *A*, *A*, dorsal aorta ; *Acd*, caudal artery ; *All*, allantoic (hypogastric) arteries ; *Am*, vitelline arteries ; *B*, truncus arteriosus ; *c*, c^1, carotids ; *D*, precaval veins (ductus Cuvieri), *E*, external iliac artery ; *Ic*, common iliac ; *KL*, gill-clefts ; *RA*, *RA*, right and left roots of the aorta, which arise from the branchial vessels *Ab*, by means of the collecting trunks, *S*, S^1 ; *Sb*, subclavian artery ; Sb^1, subclavian vein; *Si*, sinus venosus ; *V*, ventricle ; *VC*, *HC*, anterior and posterior cardinal veins ; *Vm*, vitelline veins.

extends backwards along the ventral side of the vertebral axis into the tail as a large unpaired trunk, giving off numerous branches—including paired embryonic *vitelline* or ***omphalo-***

mesenteric arteries to the yolk-sac, and (except in Fishes) *allantoic arteries* to the embryonic urinary bladder or allantois (p. 9).

Primarily, the blood becomes purified in the vessels which branch out over the yolk-sac, from whence it is returned by the *vitelline* or *omphalo-mesenteric* veins (Fig. 300). These join with the *allantoic veins* and veins of the alimentary canal to form what eventually becomes the *hepatic portal vein*, which divides up into capillaries in the liver. The capillaries then unite to form the *hepatic veins*, which open directly or indirectly into the sinus venosus.

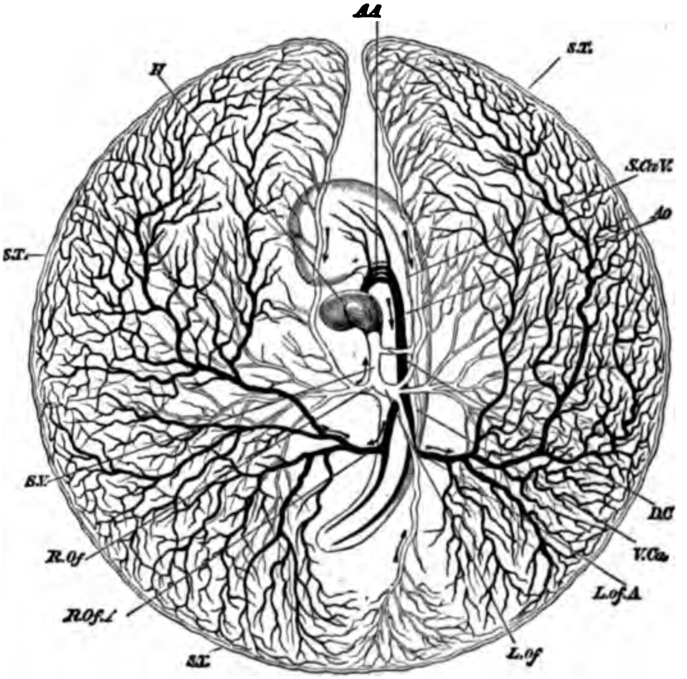

FIG. 300.—DIAGRAM OF THE CIRCULATION OF THE YOLK-SAC AT THE END OF THE THIRD DAY OF INCUBATION IN THE CHICK. (After Balfour.)

AA, the second, third, and fourth aortic arches: the first has become obliterated in its median portion, but is continued at its proximal end as the external carotid, and at its distal end as the internal carotid; *Ao*, dorsal aorta; *D.C*, ductus Cuvieri; *H*, heart; *L.Of*, left vitelline vein; *L.Of.A*, left vitelline artery; *R Of*, right vitelline vein; *R.Of.A*, right vitelline artery; *S.Ca. V*, anterior cardinal or jugular vein; *S.T*, sinus terminalis; *S.V*, sinus venosus; *V.Ca*, posterior cardinal vein. The veins are marked in outline, and the arteries are made black. The whole blastoderm has been removed from the egg, and is supposed to be viewed from below.

Into the sinus venosus there also opens on either side a *pre-caval vein* or *anterior vena cava* (*ductus Cuvieri*), which receives an *anterior cardinal* or *jugular vein* from the head, and a *posterior* *cardinal vein* from the body generally (not including the alimentary canal). The *caudal vein,* which lies directly beneath the caudal aorta, is connected with the posterior cardinals, usually indirectly, through the *renal portal veins* (cf. Figs. 325–329). The further development of the embryonic vessels may take place in one of three ways.

(1) The embryo may leave the egg, and take on an aquatic existence (Anamnia), making use of its branchial vessels for purposes of respiration, the entire allantois (Amphibia) when present giving rise to the bladder.

(2) In the Amniota, which from the first breathe by means of lungs, a modification and reduction of the branchial vessels and allantois takes place, and the latter may even disappear entirely.

(3) The embryo undergoes a longer intra-uterine existence, the allantois coming into close connection with the walls of the uterus by means of the chorionic villi: the allantoic vessels extend into the wall of the uterus and come into more or less close relations with the maternal vessels, thus serving for the respiration and nutrition of the fœtus. In this way a placenta and a placental circulation arise (pp. 9—11).

On the appearance of pulmonary respiration, important changes take place in the branchial vessels and heart. The formation of a septum both in the atrium and in the ventricle leads to the presence of two atria or auricles and two ventricles, the conus arteriosus and sinus venosus becoming eventually more or less incorporated in the right ventricle and auricle respectively. Thus a right (venous) and a left (arterial) half can be distinguished; and a new vessel, the *pulmonary artery,* arising from the last arterial arch, becomes connected with the right ventricle; this conveys venous blood to the lungs, while special vessels (*pulmonary veins*) return the oxygenated blood from the lungs to the left auricle, from which it passes into the left ventricle and so through the aorta into the general circulation of the body.

The branchial vessels never become functional, as such, in any period of development either in Sauropsida or Mammalia, but those which persist give rise, as already mentioned, to important vascular trunks of the head and neck (carotids), anterior extremities (subclavians), and lungs (pulmonary arteries), and also to the roots o the aorta, one or both of which may remain (cf. Fig. 301).

The primitive number of arterial arches is six, the first two which (belonging to the mandibular and hyoid arches respectivel almost always disappear early (Fig. 301): in caducibranchia Amphibia (including Anura) and in Amniota, the fifth arch a disappears. The third gives rise to the *carotid arch*; the fourth both sides (Amphibia, Reptilia), or of one side (Aves, Mammal to the *aortic* or *systemic arch*, and the sixth to the *pulmonary a*

From the Dipnoi onwards, the posterior cardinals become n or less completely replaced functionally by a large unpaired the *postcaval* or *posterior vena cava,* which opens independently the right auricle.

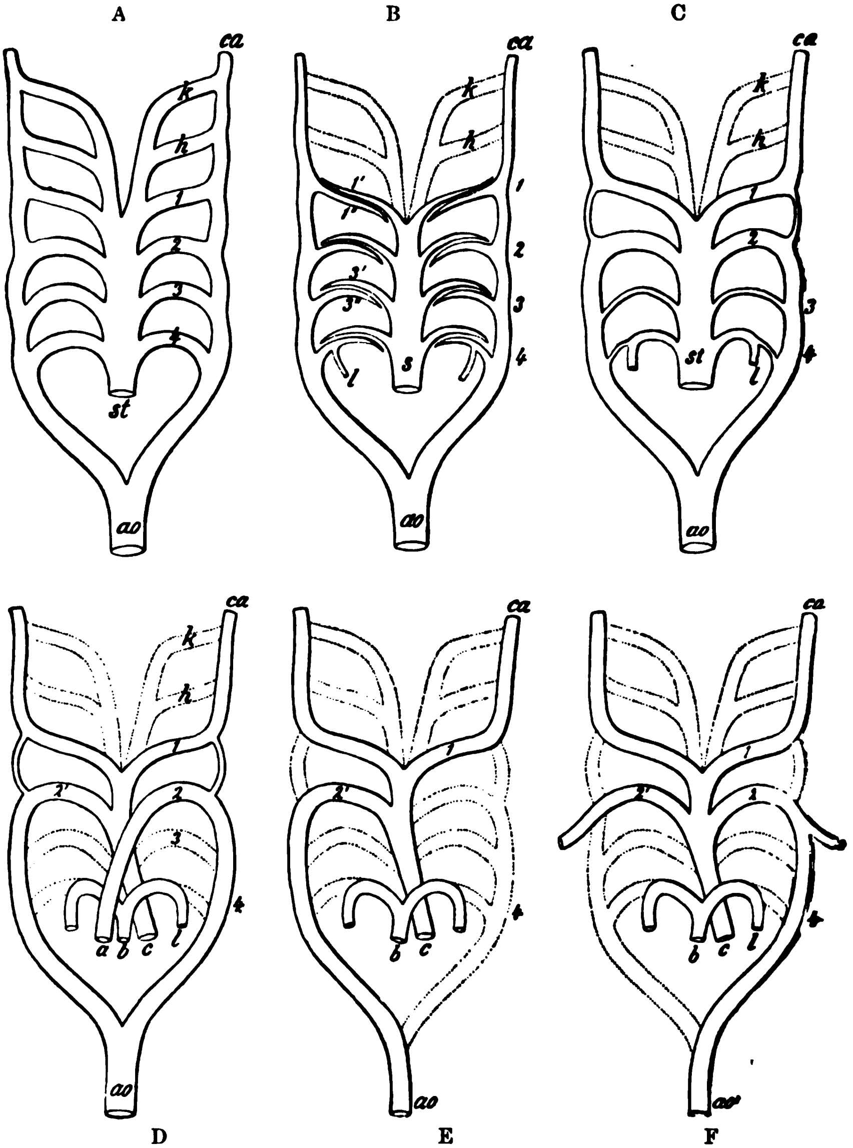

FIG. 301.—DIAGRAM OF THE ARTERIAL ARCHES OF VARIOUS VERTEBRATES, FROM THE VENTRAL SIDE. (After Boas.)

A, embryonic condition; *B*, Fish; *C*, Urodele; *D*, Reptile (Lizard); *E*, Bird; *F*, Mammal. The parts which disappear are dotted.

a, *b*, *c*, the vessels into which the ventral arterial trunk is divided in Reptiles, Birds, and Mammals; *ao*, dorsal aorta; *ca*, carotid; *k* and *h*, the two first embryonic arches, which almost always disappear; *l*, pulmonary artery; *s* (in *F*), left subclavian artery; *st*, and *s* (in *B*), ventral aorta; 1′ and 3′, first and third afferent branchial arteries; 1″ and 3″, the corresponding efferent branchial arteries; 1—4, the four branchial arches; 2 in *D* and *F*, second arch of the left side; 2′ in *D*, *E* and *F*, second arch of the right side.

THE HEART, TOGETHER WITH THE ORIGINS OF THE MAIN VESSELS.

Fishes (including **Cyclostomes**).—The heart in Fishes is situated in the anterior part of the body-cavity, close behind the head. It consists of a ventricle, with a truncus arteriosus or merely a bulbus (Cyclostomi, most Teleostei), and an atrium or auricle, the latter receiving its blood from a sinus venosus, and being laterally expanded to form the *appendices auriculæ* (Figs. 302 and 303.)

In correspondence with the work which each portion has to perform, the walls of the atrium are comparatively thin, while those of the ventricle are much stronger, its muscles giving rise in the interior to a muscular network in which a series of larger trabeculæ can usually be recognised: this holds good throughout the Craniata.

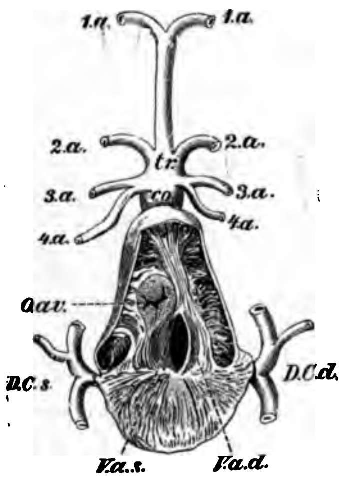

FIG. 302.—HEART OF *Acanthis vulgaris*, FROM THE DORSAL SIDE, WITH THE ATRIUM CUT OPEN. (After Röse.)

Co, *tr*, truncus anteriosus ; *D.C.d* and *D.C.s*, right and left precavals ; *O.a.v*, atrio-ventricular aperture ; *V.a.d.* and *V.a.s*, right and left valve of the sinus venosus ; 1*a*—4*a*, afferent branchial arteries.

Between the sinus venosus and atrium, and also between atrium and ventricle, membranous valves are present; there are primarily two atrioventricular valves, but they may become further subdivided. Numerous valves, arranged in rows, are present in the muscular conus arteriosus (Fig. 303, A): these are most numerous in Elasmobranchs and Ganoids. There is a tendency, however, for the posterior valves, or those which lie nearest the ventricle, gradually to undergo reduction (B). Only the most anterior row persists between the ventricle and bulbus in Cyclostomes and most Teleosts (C), but amongst the latter two rows are retained in the vestigial conus in Albula (Butirinus) and Tarpon.

The heart of all Fishes except Dipnoans contains venous blood only, which it forces through the afferent branchial arteries (Figs. 302, 320, 321) into the capillaries of the gills, where it becomes oxygenated, to pass thence into the efferent branchial arteries, and so into the dorsal aorta.

The heart of the Dipnoi (Figs. 304 and 305), in correspondence with the double mode of respiration (by lungs as well as by gills) reaches a higher stage of development, mid-way between that seen in Elasmobranchs and in Amphibians, and nearly resembling that of Urodeles. The atrium becomes divided into a *left* and *right* chamber by a septum: this is also true of the ventricle to some extent, owing to the presence of a cushion composed of muscular fibres and fibro-cartilage arising from the margin of the sinu-atrial aperture, extending into the atrium and ventricle, and acting as a valve, ordinary atrioventricular valves being absent. The sinus venosus, from the Dipnoi onwards, opens into the right atrium.

The conus arteriosus is twisted spirally on itself: in Ceratodus it is provided with eight transverse rows of valves, and begins to be divided into two chambers. In Protopterus this division is complete, so that two currents of blood, mainly arterial and mainly venous respectively, pass out from the heart side by side. The former comes from the pulmonary vein, from which it passes into the left atrium, thence into the left portion of the ventricle, and thence to the two anterior branchial arteries. The venous current, on the other hand, passes from the right portion of the ventricle into the third and fourth afferent branchial arteries and thence to the corresponding gills, where it becomes purified; it reaches the aortic roots by means of the efferent branchial arteries. The paired *pul-*

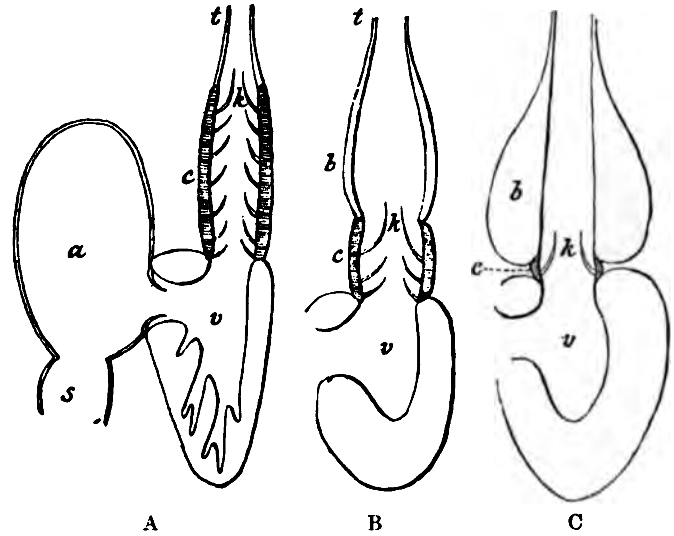

FIG. 303.—DIAGRAMMATIC LONGITUDINAL SECTIONS THROUGH THE HEARTS OF VARIOUS FISHES. (From Boas's *Zoology*.) *A*, Fish with well-developed conus arteriosus (*e.g.* Elasmobranch); *B*, Amia; *C*, Teleost. In *B* and *C* the sinus venosus and atrium are not indicated.

a, atrium; *b*, bulbus arteriosus; *c*, conus arteriosus; *k*, valves; *s*, sinus venosus; *t*, ventral aorta; *v*, ventricle.

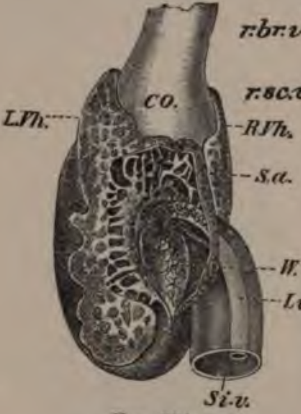

FIG. 304.

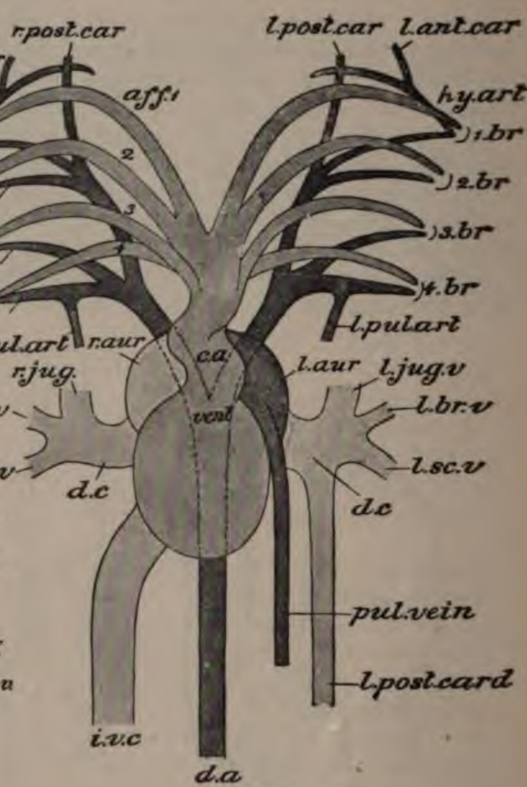

FIG. 305.

FIG. 304.—HEART OF *Protopterus annectens*. From the left side, part of the wall of the left atrium being removed. (After Röse.)

Co, conus arteriosus; *L. Vh* and *R. Vh*, left and right atria; *S.a*, septum atriorum; *Si.v*, sinus venosus, within which the pulmonary vein (*Lv*) extends to open into the left auricle by a valvular aperture; *W*, fibrous cushion extending into the ventricle.

FIG. 305.—*Ceratodus forsteri*. DIAGRAMMATIC VIEW OF THE HEART AND MAIN BLOOD VESSELS AS SEEN FROM THE VENTRAL SURFACE. (From Parker and Haswell's *Zoology*, after Baldwin Spencer.)

aff. 1, 2, 3, 4, afferent branchial arteries; 1 *br*, 2 *br*, 3 *br*, 4 *br*, position of gills; *c.a*, conus arteriosus; *d.a*, dorsal aorta; *d.c*, ductus Cuvieri; *epi.*1, *epi.*2, *epi.*3, *epi.*4, efferent branchial arteries; *hy.art*, hyoidean artery; *i.v.c*, postcaval vein; *l.ant.car*, left anterior carotid artery; *l.aur*, left auricle *l.br.v*, left brachial vein; *l.jug.v*, left jugular vein; *l.post.car*, left posterior carotid artery; *l.post.card*, left posterior cardinal vein: *l.pul.art*, left pulmonary artery; *l sc.v*, left sub-scapular vein; *r.ant car*, right anterior carotid artery; *r.aur*, right auricle; *r.br.v*, right brachial vein; *r.jug.*, right jugular vein; *r.post.car*, right posterior carotid; *r.pul.art*, right pulmonary artery; *r.sc.v*, right subscapular vein; *vent*, ventricle.

monary artery like the corresponding vessel in Crossopterygians, arises from the fourth efferent branchial in Ceratodus

(Fig. 305), and from the aortic root in Protopterus and Lepidosiren, that of the right side bifurcating to supply the dorsal surface of the lung, while that of the left side supplies the ventral surface. The two pulmonary veins unite to form a median trunk which becomes closely connected with the sinus venosus, so as to appear sunk within its walls in the form of two valve-like projections[1] (Fig. 304). Thus the blood once more becomes purified before it passes into the left side of the ventricle. A *post-caval* vein, present from the Dipnoi onwards, opens into the sinus venosus posteriorly to the precavals, and with it the hepatic veins communicate (Figs. 305 and 328).

Amphibians.—With the exception of the Gymnophiona, the heart in all Amphibians lies far forwards, below the anterior vertebræ. A septum atriorum is present,[2] but in Urodela and Gymnophiona it is more or less fenestrated (Fig. 307): it never completely separates the cavities of the two atria, and forms an arch over the atrioventricular aperture. There are always two sinu-atrial valves and two atrio-ventricular valves, the latter of which are connected with the walls of the ventricle by cords. The two pulmonary veins unite before opening obliquely, as in all the higher Vertebrates, into the left atrium, at which point there are no special valves: the two precavals and the postcaval open independently into the sinus venosus.

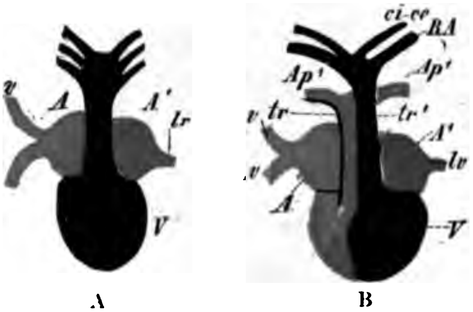

FIG. 306.—DIAGRAM SHOWING THE COURSE OF THE BLOOD THROUGH THE HEART IN *Urodela* (A) AND *Anura* (B).

A, right atrium ; *A*¹, left atrium ; *lr*, *lv*, pulmonary veins ; *tr*, conus arteriosus, divided in Anura (B) into two portions, *tr*, *tr*¹ : through *tr* venous blood passes into the pulmonary arteries, *Ap*¹, *Ap*¹, while through *tr*¹ mixed blood goes to the carotids, *ci—ce*, and to the roots of the aorta, *RA* ; *V*, ventricle ; *v*, *v*, pre- and postcavals (only one precaval is indicated).

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[1] The largest of these, as well as the fibrous cushion described above, take a greater part in separating the two auricles than does the septum proper.

[2] In the lungless Urodeles (cf. p. 378) the septum atriorum and pulmonary vein are wanting, though the pulmonary artery can still be recognised.

Neither in Urodela nor Anura is there a septum ventriculorum, so that the blood passing out from the spongy ventricle must have a mixed character (Fig. 306). The ventricle is usually short and compressed, but is more elongated in Amphiuma, Proteus, and the Gymnophiona. It is continued anteriorly into a conus arteriosus; this has usually a slight spiral twist, and possesses a transverse row of valves at either end, as well as a spiral fold, formed by a fusion of valves and extending into its lumen, thus partially dividing it into a dorsal *cavum pulmonale*, and a ventral *cavum aorticum* communicating with the carotid and systemic arches. This holds good, *e.g.*, for Amblystoma, Salamandra, Amphiuma, and Siren. In others (*e.g.* Necturus, Proteus, Gymnophiona), the conus is more elongated, and reduction is seen in the disappearance of the spiral fold and the presence of only a single row of valves.

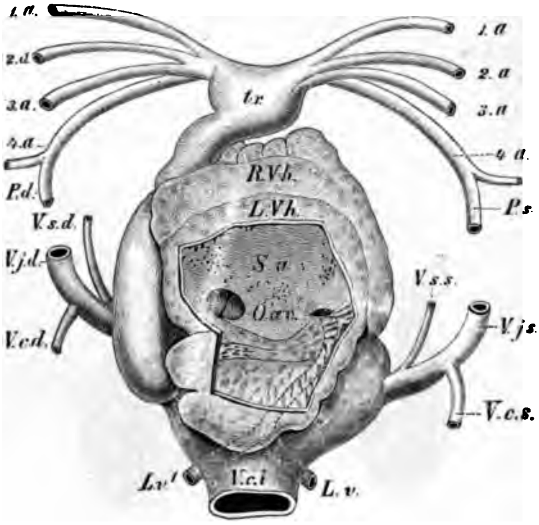

FIG. 307.—HEART OF *Cryptobranchus japonicus*. From the ventral side. (After Röse.) The left atrium is cut open.

L.v, $L.v^1$, the two pulmonary veins, opening by a single aperture into the left atrium; *L.Vh*, *R.Vh*, left and right atria; *O.av*, atrio-ventricular aperture; *P.d* and *P.s*, left and right pulmonary arteries; *S.a*, septum atriorum, perforated by numerous small apertures; *tr*, truncus arteriosus; *V.c.d* *V.c.s*, posterior cardinal veins; *V.c.i*, postcaval vein; *V.j.d* and *V.j.s*, jugular veins; *V.s.d* and *V.s.s*, subclavian veins; 1^a, 4^a, the four arterial arches.

In Anura, the fold lying within the conus extends so far back that no undivided portion of the cavity is left. The consequence of this is that the blood passing into the hindermost pair of the arterial arches—that from which the pulmonary arteries arise—is mainly venous, while the others contain more or less mixed blood

(Fig. 306, B); for, owing to the spongy nature of the ventricle, there is no time for its contained blood to get thoroughly mixed before it is forced into the conus.[1]

As in the Dipnoi, four afferent branchial arteries arise on either side in the Amphibia, which—taking as a type the larva of Salamandra—have the following relations (cf. Fig. 301, C). The three anterior arteries pass to a similar number of external gill-tufts, in which they break up into capillaries (Fig. 308). From the latter three efferent vessels arise, which pass to the dorsal side, and there unite on either side to form the aortic root. The fourth afferent branchial artery, which is smaller than the others, does not pass to a gill, but to the pulmonary artery, which arises from the efferent branchials. The pulmonary artery, therefore contains far more arterial than venous blood, and thus the lungs of the Salamander larva, like the swim-bladder of Fishes, can only be of secondary importance in respiration.

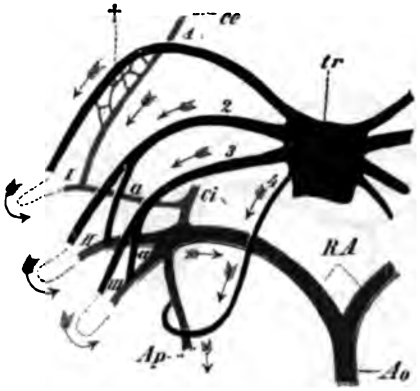

FIG. 308.—THE ARTERIAL ARCHES OF THE LARVA OF A SALAMANDER. From the ventral side. Slightly diagrammatic. (After J. E. V. Boas.)

a,*a*, direct anastomoses between the second and third afferent and efferent branchial arteries; *Ao*, dorsal aorta; *ce*, external carotid; *ci*, internal carotid; *RA*, aortic roots; *tr*, truncus arteriosus; 1—3, the three afferent branchial arteries; *I—III*, the corresponding efferent arteries; 4, the fourth arterial arch, which becomes connected with the pulmonary artery (*Ap*); †, net-like anastomoses between the external carotid and the first afferent branchial artery, which gives rise later to the carotid labyrinth. The arrows show the course which the blood takes.

The internal carotid arises from the first efferent branchial artery, towards the middle line, the external carotid coming off further outwards (Fig. 308). The latter, as it passes forwards, becomes connected with the first afferent branchial by net-like anastomoses, which later, losing the character of a network or *rete mirabile*, gives rise in the adult to a swelling, the *carotid labyrinth* (so-called "carotid gland"), which consists simply of a muscular vesicle with septa in its interior, and probably acts as an accessory heart. Direct connections exist, however, between the second and third afferent and efferent arteries.

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[1] Special vessels supplying the walls of the heart are apparently wanting in the case of many Fishes and of Amphibians. In Elasmobranchs, *coronary arteries* arise from the hypobranchial artery and *coronary veins* open into the sinus venosus or auricle; similar vessels have also been described in certain Ganoids and Teleosts. Coronary veins occur in Cryptobranchus japonicus.

Towards the end of the larval period, the second efferent branchial artery increases considerably in relative size, and the fourth arterial arch also becomes larger. By a reduction of the anastomosis with the third arch, the fourth carries most of the blood for the pulmonary artery, and the latter thus now contains more venous than arterial blood. When branchial respiration ceases, the anastomosis between each corresponding afferent and efferent branchial artery no longer consists of capillaries, but a direct connection between them becomes established (Fig. 309). Finally, the connection between the first and second arches disappears, the former giving rise to the carotid and the latter forming the large aortic root; an anastomosis remains throughout life, however, between the fourth arch, which forms the pulmonary artery, and the second and third arches. This is usually spoken of as the *ductus Botalli*. The third arch varies greatly in its development: it may be present on one side only, or may even be entirely wanting (*e.g.* Triton). In the larvæ of Anura there are also four afferent branchial arteries present on either side, but these are connected with the corresponding efferent vessels by capillaries

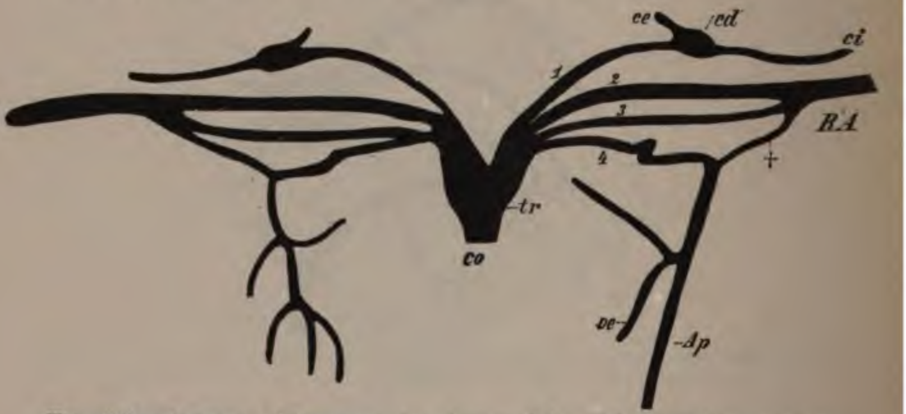

FIG. 309.—ARTERIAL ARCHES OF AN ADULT *Salamandra maculosa*, SHOWN SPREAD OUT. (After J. E. V. Boas.)

cd, carotid labyrinth; *ce*, external carotid; *ci*, internal carotid; *co*, *tr*, truncus arteriosus; *œ*, œsophageal vessels; *RA*, root of the aorta; 1—4, the four arterial arches. The fourth arterial arch, which gives rise to the pulmonary artery (*Ap*), has increased considerably in size relatively, and is only connected by a delicate ductus Botalli (†) with the second and third arches.

only, there being no direct anastomoses. The consequence of this is that *all* the blood becomes oxygenated. In the adult Frog the third arterial arch is entirely obliterated, and there is no ductus Botalli: the other vessels resemble those of the Salamander.

Reptiles.—As in all Amniota, the heart of Reptiles arises far forwards in the neighbourhood of the gill-clefts, but on the formation of a neck it comes to lie relatively further back than in the Anamnia, and this is more especially the case in Amphisbænians, Snakes, and Crocodiles. The carotid arteries and jugular veins are thus correspondingly elongated.

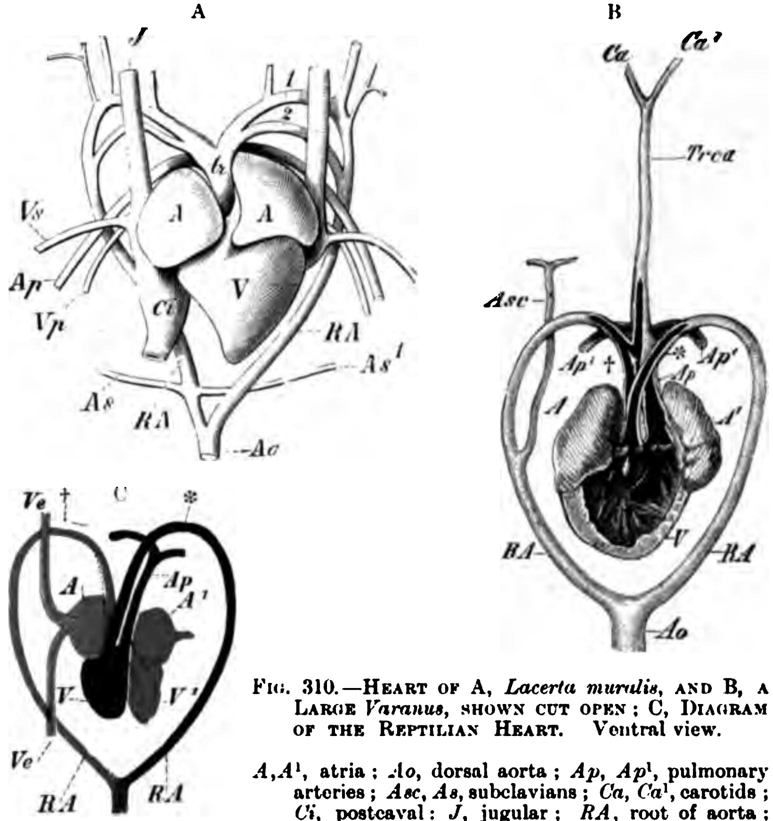

FIG. 310.—HEART OF A, *Lacerta muralis*, AND B, A LARGE *Varanus*, SHOWN CUT OPEN; C, DIAGRAM OF THE REPTILIAN HEART. Ventral view.

A, A^1, atria; *Ao*, dorsal aorta; *Ap*, Ap^1, pulmonary arteries; *Asc*, *As*, subclavians; *Ca*, Ca^1, carotids; *Ci*, postcaval: *J*, jugular; *RA*, root of aorta; *tr*, *Trca*, innominate; *Vp*, pulmonary vein; *Vs*, subclavian vein; *V*, V^1, ventricles; *1*, *2*, 1st and 2nd arterial arches; †, *, right and left aortic arches. In C, the pre- and postcavals are indicated by *Ve*, *Ve*, only one precaval being represented. A fibrous cord connects the apex of the ventricle with the pericardium in most Lizards.

The sinus venosus, which even in the Amphibia—especially

Anura—shows indications of becoming sunk into the right atrium is now usually no longer recognisable as a distinct chamber externally, though it still persists, with the two typical valves (cf. Figs. 311–313). It becomes partially divided into two portions by a septum, on the left of which the left precaval opens: this subdivision of the sinus, hardly indicated in Chelonians, is well marked in Crocodiles, and is complete in Birds and Mammals. The pulmonary veins unite into a single trunk before entering the left atrium.

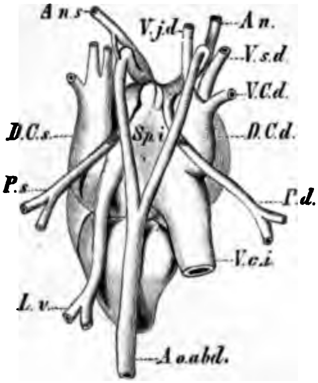

Fig. 311.—Heart of *Cyclodus boddaertei*. From the dorsal side. (After Röse.)

An, *An.s*, innominate arteries; *Ao.abd*, dorsal aorta; *D.C.d*, *D.C.s*, precaval veins; *L.v*, pulmonary vein; *P.s*, *P.d*, pulmonary arteries; *Sp.i*, spatium intersepto-valvulare (cf. Fig. 316); *V.C.d*, posterior cardinal; *V.j.d*, jugular, and *V.s.d*, subclavian vein of the right side; *V.c.i*, postcaval vein.

The atrial septum is solid and unperforated; and, as its margin reaches much further posteriorly towards the ventricle than in Amphibians, it not only completely separates the two atria, but also divides the atrio-ventricular aperture into two. The two primarily dorsal and ventral atrio-ventricular valves, moreover, become fused together and then again subdivided in the plane of the atrial septum, so that a right and left valve are now seen.[1]

The principal advance in structure as compared with the amphibian heart is, however, seen in the appearance of a muscular *ventricular septum*, which may be incomplete (Hatteria, Lizards, Snakes, Chelonians), or complete (Crocodiles). The higher Lizards (*e.g.* Varanidæ, Fig. 310, B) come nearest the Crocodiles in this respect, but in no Reptiles except the latter is there more than a periodic physiological separation between the two halves of the ventricle. A complete septum ventriculorum thus appears for the first time in Crocodiles (Fig. 314), in which consequently the right ventricle contains unmixed venous blood, and the left ventricle unmixed oxygenated blood, although, as will be seen presently, an admixture takes place in the systemic arteries. In Crocodiles the right atrio-ventricular aperture is guarded by a large muscular flap on the right (outer) side of the aperture.

The conus arteriosus now becomes practically absorbed into the ventricular portion of the heart, and each aortic root may be made up at its origin of two arches, anastomosing with one another (Lacerta, Fig. 310, A), or of one only (certain Lizards, Snakes, Chelonians, and Crocodiles, Figs. 310, B, 312), from which the carotid artery arises directly. The left and right aortic arches cross at their base, so that the left arises on the right side, and *vice versa.* The most posterior arterial arch gives rise to the pulmonary artery (cf. Fig. 301, D).

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[1] In Ascalabota (*e.g. Tarentola mauritanica*) and Chelonia the proximal part of the aortico-pulmonary septum encloses a plate of hyaline cartilage (cartilage of Bojanus), and cartilages may occur in the neighbourhood of the semilunar valves the aorta and pulmonary artery in other Reptiles (*e.g.* Crocodiles).

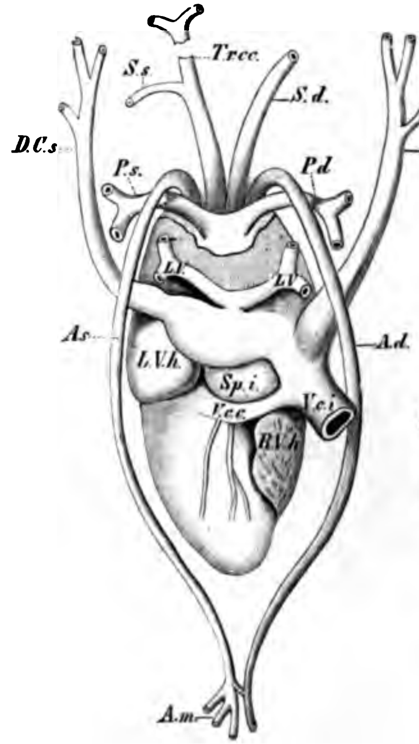

FIG. 312.

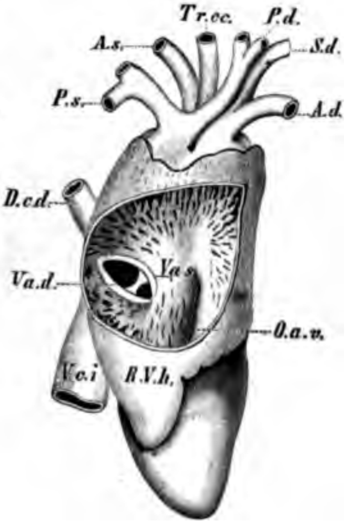

FIG. 313.

FIG. 312.—HEART OF A YOUNG *Crocodilus niloticus.* From the dorsal side. (After Röse.)

A.d and *A.s*, right and left aortic arches; *A.m*, mesenteric artery; *L.V.h*, *R.V.h*, left and right atria; *S.d*, *S.s*, subclavian arteries; *Tr.cc*, common carotid; *V.c.c*, coronary vein. Other letters as in Fig. 311.

FIG. 313.—HEART OF *Crocodilus niloticus.* From the right side. (After Röse.) Part of the wall of the right atrium is removed.

O.a.v, atrio-ventricular aperture; *Va.d* and *Va.s*, the two sinu-auricular valves, the white line between which is the margin of the septum sinus venosi. Other letters as in Figs. 311 and 312.

The blood from the right ventricle passes into the pulmonary artery as well as into the left aortic arch, and, according as the septum ventriculorum is complete or incomplete, is either entirely venous (Crocodiles) or mixed (other Reptiles). Thus even in Crocodiles, although unmixed venous blood passes to the lungs, the systemic arteries contain mixed blood; moreover, a small aperture of communication (the *foramen of Panizza*) exists between the two aortic roots at their origin, just distal to the valves (Fig. 314). The valves at the base of the main arterial stems have undergone a considerable reduction in Reptiles as compared with lower forms; there is only a single row at the origin of each aorta and the pulmonary artery. Coronary vessels re well developed.

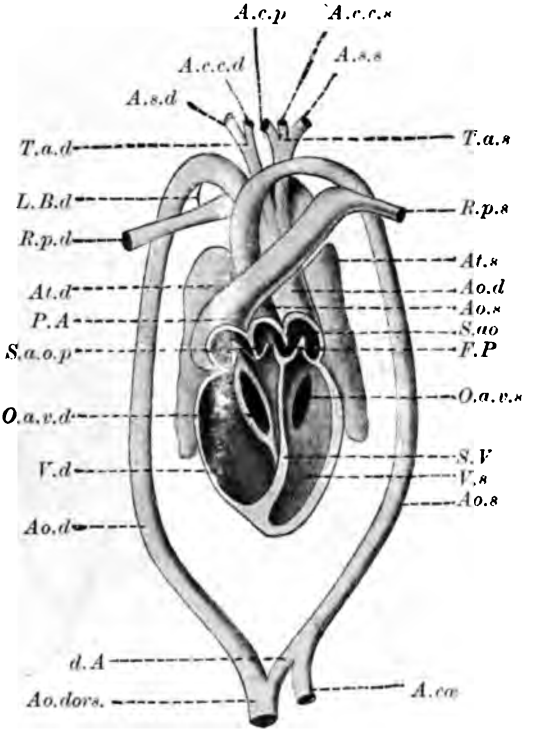

FIG. 314.—DIAGRAM OF THE HEART OF A CROCODILE. Ventral view. (After A. Greil.)

Ac.c.d and *Ac.c.s*, right and left collateral artery; *A.c.p*, prevertebral carotid; *A.cœ*, cœliac; *Ao.d*, *Ao.s*, right and left aortic arches or roots; *Ao.dors*, dorsal aorta; *A.s.d* and *A.s.s*, right and left subclavian; *At.d* and *At.s*, right and left atrium; *d.A*, so-called dorsal anastomosis of the two aortic arches; *F.P*, foramen of Panizza; *L.B.d*, right ligamentum Botalli; *O.a.v.d* and *O.a.v.s*, right and left atrio-ventricular ostium; *P.A*, root of pulmonary artery; *R.p.d* and *R.p.s*, right and left pulmonary artery; *S.ao*, aortic septum; *S.ao.p*, aortico-pulmonary septum; *S.V*, ventricular septum; *T.a.d* and *T.a.s*, right and left innominate; *V.d* and *V.s*, right and left ventricle.

Birds and Mammals.—In these Classes, the atrial and ventricular septa are always complete, and there is no longer any mixture of the arterial and venous blood. The muscular walls of the ventricle are strongly developed and very compact. This is particularly the case in the left ventricle, on the inner wall of which the *papillary muscles* are very strong: the left ventricle is partially surrounded by the right, the cavity of the latter having a semilunar transverse section, and its walls being much thinner than those of the former (Fig. 315).

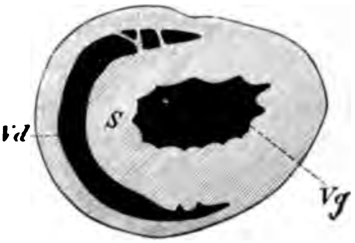

FIG. 315.—TRANSVERSE SECTION THROUGH THE VENTRICLES OF *Grus cinerea*.

S, septum ventriculorum; *Vd*, right, and *Vg*, left ventricle.

Both in Birds and Mammals the blood from the head and body passes by means of the precavals and postcaval into the right atrium,[1] as does also that from the walls of the heart through the coronary veins,[2] and the sinus venosus—especially in Mammals—is scarcely recognisable (Figs. 316–318): the right atrium is separated from the right ventricle by means of a well-developed valve. In Birds this valve, like that of Crocodiles, is very large and muscular, while in most Mammals it consists of three membranous lappets (tricuspid valve) to which are attached tendinous cords, arising from the papillary muscles. In Birds and Monotremes the left atrio-ventricular aperture is provided with a valve consisting of three membranous folds: in other Mammals there are only two folds, and the valve is therefore known as the *bicuspid* or *mitral*.[3] Three semilunar pocket-like valves are also present at the origins of the pulmonary artery and aorta both in Birds and Mammals.

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[1] Considerable variations are seen in Birds in this respect; all three veins may open together, or separately; or again, the left precaval may open independently, and the right precaval and postcaval together.

[2] These open into the base of the left precaval (*coronary sinus*), the rest of which disappears in certain Mammals. Coronary arteries are also present, arising from the base of the aorta.

[3] There are no chordæ tendineæ in Monotremes, the heart of which in many other respects resembles that of the Sauropsida. One of the lappets on either side is attached to the septum; on the left side there is one lateral lappet, and on the right two. In Marsupials, the number of lappets in the "tricuspid" valve varies between two and five. As regards the papillary muscles, the following may be taken as a type in Placental Mammals. In the right ventricle the two lateral lappets are connected with three papillary muscles or groups of muscles; of these the strongest is lateral, arising from the septum or from the outer wall of the ventricle, the others being respectively ventral and dorsal, the latter of which is the weakest of the three. The median lappet is usually connected by chordæ tendineæ directly to the septum, at which point small papillary muscles may be present. In the left ventricle there is a ventral and a dorsal group of papillary muscles, from which the chordæ tendineæ exclusively arise; the lateral valve is also connected directly with the lateral wall of the ventricle by a few tendinous cords.

As regards the origin of the great vessels, Birds are distinguished from Mammals by the fact that in them the *right*, while in Mammals the *left*, aortic arch persists (Fig. 301, E, F); the corresponding arch of the other side in both cases takes part in forming the subclavian artery. Thus both in Birds and Mammals there is only a single aortic arch. As in Amphibians, the posterior arterial arch gives rise to the pulmonary artery.

The pulmonary veins, two from each lung, open close together into the left atrium (Fig. 317).

Amongst the more important points in the development of the heart may be mentioned the fact that in the embryo the two atria communicate with one another by means of an aperture, the *foramen ovale*, or by several apertures, formed secondarily in the atrial septum, through which the venous blood from the right atrium passes directly into the left atrium (Fig. 318). This foramen becomes closed later by secondary growths, which are less complicated in Birds and Monotremes than in Placental Mammals, in which a secondary circular septum is found, and when the lungs

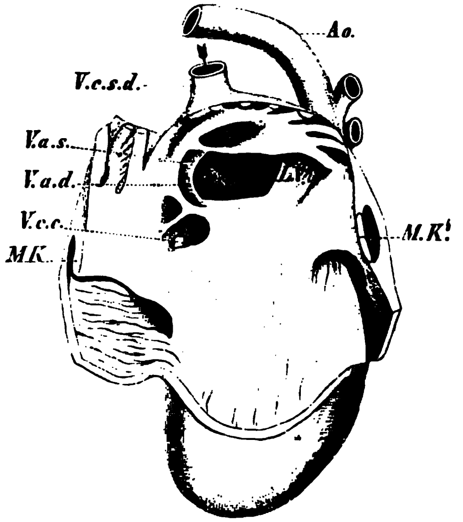

FIG. 316.—HEART OF GOOSE (*Anser vulgaris*), DISSECTED FROM THE RIGHT SIDE. (After Röse.)

The right atrium and ventricle are cut open, and their walls reflected. ***Ao***, aorta; *L. Vi*, limbus fossæ ovalis (Vieussenii)—a ridge arising from the ventral wall of the right atrium: the space between this and the septum atriorum is known as the spatium intersepto-valvulare (cf. Figs. 311 and 312). ***MK***, ***MK***^{1}, muscular right atrio-ventricular valve; *S.a*, septum atriorum; ***V.a.d.*** *V.a.s*, the two sinu-auricular valves, situated at the entrance of the postcaval; *V.c.c*, aperture of coronary vein; *V.c.s.d*, right precaval.

come into use, its position can still be recognised as a thin area (*fossa ovalis*) in the atrial septum, surrounded by a circular

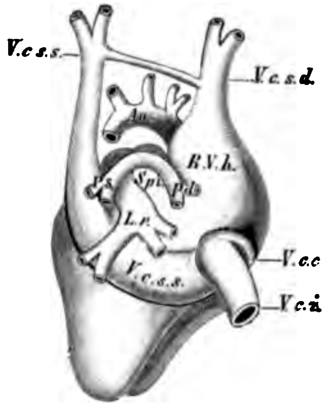

FIG. 317.—HEART OF *Ornithorhynchus paradoxus*. From the dorsal side. (After Röse.)

Ao, aorta; *L.v*, pulmonary veins; *P.d*, *P.s*, pulmonary arteries; *R.V.h*, right atrium; *Spi*, Spatium intersepto-valvulare; *V.c.c*, coronary vein; *V.c.i*, postcaval; *V.c.s.s*, coronary sinus; *V.c.s.s*, *V.c.s.d*, precaval veins.

ridge (*annulus ovalis*). Extending from this to the base of the postcaval and right precaval respectively are two more or less well-marked folds, known as the postcaval (*Eustachian*) valve and the valve of the coronary sinus (*Thebesian* valve) respectively (Fig.

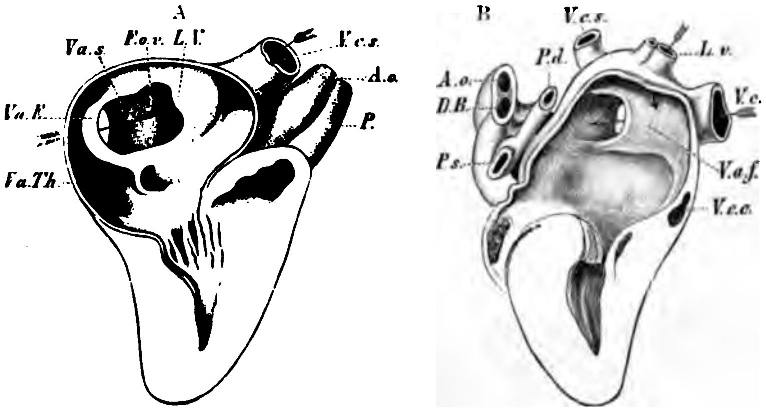

FIG. 318.—HEART OF HUMAN FOETUS (8TH MONTH). A, from the right, and B, from the left side. (After Röse.) The walls of the atrium and ventricle are partly removed in each figure.

A.o, aorta; *D.B*, ductus Botalli (ductus arteriosus); *F.o.v*, foramen ovale; *L.V*, left atrium; *L.v*, pulmonary vein; *P*, *P.d*, *P.s*, pulmonary artery; *Va.s*, left sinu-auricular valve, fused with the septum atriorum (*Sa*, *V.a.f*); *Va.Th*, Thebesian valve, in direct connection with the Eustachian valve (*Va.E*); *V.c.c*, coronary vein; *V.c.i*, postcaval; *V.c.s*, left precaval.

318, A); these represent the remains of the sinu-auricular **valves,** and in the embryo aid in conducting the blood from the **right** atrium into the left.[1]

Great variations are seen in the mode of origin of the **carotids** and subclavians from the arch of the aorta in **Mammals. For** example, there may be a *brachiocephalic* or *innominate trunk* on

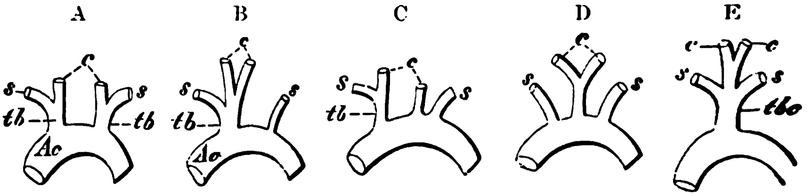

FIG. 319.—FIVE DIFFERENT MODES OF ORIGIN OF THE GREAT VESSELS FROM THE ARCH OF THE AORTA IN MAMMALS.

Ao, aortic arch ; *c*, carotids ; *s*, subclavians ; *tb*, *tbc*, brachiocephalic trunk.

either side (Fig. 319, A); an unpaired common brachiocephalic, from which the carotid and subclavian of one or both sides arise (B, C, E); or a common trunk of origin for the carotids, the subclavians arising independently on either side of it (D).

ARTERIAL SYSTEM.

In Amphioxus, the ventral aorta, as in the Craniata, gives off a series of *afferent branchial arteries*, which are, however, in correspondence with the greater number of gill-clefts, much more numerous than in other Vertebrates. The afferent branchial vessels pass up the primary gill-bars, and give off branches to the secondary gill-bars (Fig. 258). and both series of branchial vessels open dorsally, as *efferent branchial arteries*, into a *dorsal aorta* on either side. The latter unites with its fellow posteriorly to the pharynx to form a median dorsal aorta, which gives off branches to the intestine, &c.

The essential relations of the carotid arteries, dorsal aorta, and pulmonary arteries in the Craniata, as well as of the embryonic vitelline arteries, have already been dealt with. Two carotids (usually described as anterior and posterior, or as internal and external) can usually be recognised in Fishes, arising independently on either side from the anterior afferent branchial arteries, but varying much in their arrangement (Figs. 304, 320, 321): there may also be a ventral *mandibular* or *lingual* artery. From the Amphibia onwards, internal and external carotids are formed by the bifurcation of each *common carotid*. In these higher types, the internal carotid passes entirely into the cranial cavity, and supplies the brain with blood, while the external carotid goes to the external parts of the head (face, tongue, and muscles of mastication).

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[1] Ossifications may occur in the neighbourhood of the atrio-ventricular and arterial apertures in various Ungulates.

In Fishes a series of nutrient branchial vessels arise in connection with a hypobranchial artery formed by the union of vessels given off from the ventral ends of the afferent branchial arteries (Figs. 320, 321, and cf. note on p. 405).

The origin of the subclavian artery,[1] which supplies the anterior extremity, is very inconstant, being sometimes symmetrical, sometimes asymmetrical. It arises either in connection with the posterior afferent branchial vessels, or from the roots or main trunk of the aorta. Extending outwards towards the free extremity, the subclavian passes into the *brachial artery*, which in higher forms divides into an ulnar and a radial branch, and these again subdivide to form the arteries of the manus. The condition seen in lower forms and in certain embryonic stages of higher types shows that these vessels arise from networks, which occur more particularly along the larger nerve-trunks. Each main vessel is therefore merely a more strongly developed portion of a connected system of canals which, especially in the axillary region, is seen to be formed originally from segmental vessels connected by longitudinal anastomoses.

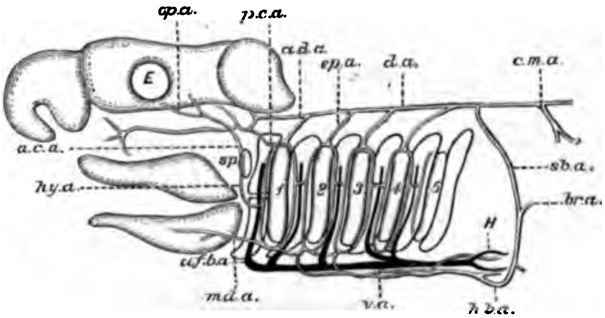

FIG. 320.—DIAGRAM OF THE BRANCHIAL ARTERIAL SYSTEM OF *Mustelus antarcticus*. Left lateral view. (From Bridge, after T. J. Parker.)

The ventral aorta and afferent branchial vessels are in solid black; the afferent arteries and their branches have double contours. The branchial clefts have fringed borders to indicate their hemibranchs, and the arches are in simple outline.

a.c.a, anterior (ventral) carotid; *a.d.a*, anterior dorsal aorta; *af.b.a*, afferent branchial; *br.a*, brachial; *c.m.a*, cœliaco-mesenteric; *d.a*, dorsal aorta; *E*, eye; *ep.a*, epibranchial; *H*, heart; *h.b.a*, hypobranchial; *hy.a*, afferent pseudobranchial or hyoidean; *md.a*, mandibular; *op.a*, ophthalmic; *p.c.a*, posterior (dorsal) carotid; *sb.a*, subclavian; *sp*, spiracle; *v.a*, ventral aorta; 1—5, the hyobranchial and four succeeding branchial clefts.

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[1] In the Amphibia the great cutaneous artery, arising from the subclavian, extends backwards, anastomoses with the epigastric artery, and gives off numerous branches to the skin.

From the dorsal aorta arise *parietal* (*intercostal, lumbar*), and *cœliac, mesenteric,* and *urinogenital* arteries, supplying the body-walls and viscera respectively. These all vary greatly both in number and relative size: thus, for instance, there is sometimes a single cœliaco-mesenteric artery, sometimes a separate cœliac, and one or more mesenteric arteries (Figs. 322 and 323).[1] The *renal* and *genital arteries* also vary in number and arrangement. All the branches of the dorsal aorta, however, present primarily an approximately metameric character, their number becoming more or less reduced owing to a concentration of the vessels, which is more marked in short-bodied than in long-bodied Vertebrates. In other cases a reduction in the number of vessels takes place by the formation of anastomoses, one branch taking to itself the peripheral twigs of another branch, so that the main stem of the latter disappears.[2]

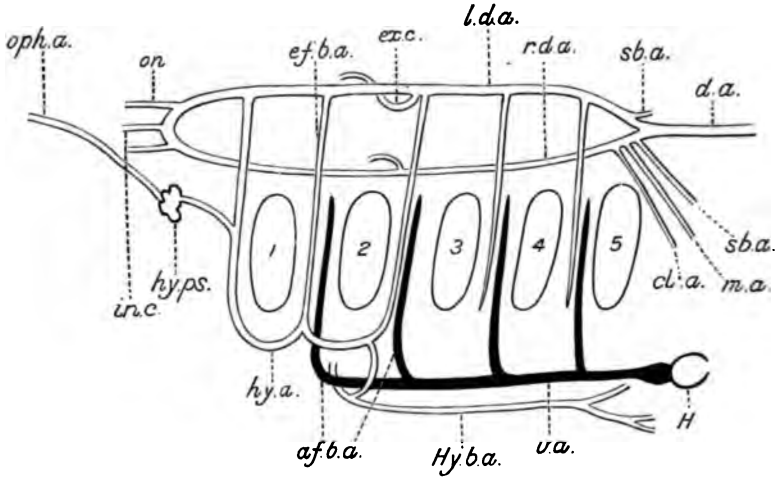

FIG. 321.—BRANCHIAL ARTERIAL SYSTEM OF COD (*Gadus morrhua*). Lateral view. (From Bridge, altered from T. J. Parker.)

af.b.a, 1st and 2nd afferent branchial; *cl.a,* cœliac; *d.a,* median dorsal aorta; *ef.b.a,* first afferent branchial; *ex.c,* "external" carotid; *H,* heart; *hy.a,* hyoidean; *Hy.b.a,* hypobranchial (to heart and pelvic fins); *hy.ps,* spiracular pseudobranch; *in.c,* "internal" carotid; *l.d.a,* left suprabranchial; *m.a,* mesenteric; *on,* orbitonasal; *oph.a,* ophthalmic; *r.d.a,* right suprabranchial; *sb.a,* subclavian; *v.a,* ventral aorta; 1—5, hyobranchial and succeeding gill-clefts.

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[1] The *cœliac* typically supplies the stomach, liver, and spleen; one or more *anterior mesenterics* the whole intestine with the exception of the rectum, as well as the pancreas; and a *posterior mesenteric* the rectum. In Hatteria a very primitive arrangement of the branches of the aorta is retained.

[2] Special mention must be made of the *collateral vertebral artery,* which in Urodeles arises on either side from the root of the aorta and extends backwards along the vertebral column to the end of the tail (Fig. 322). At the base of the transverse processes numerous branches extend from it into the vertebral canal, while others pass along the ribs and reach as far as the skin; it also communicates with the aorta along its entire length.

The aorta is continued posteriorly into the *caudal artery*, which usually lies within a cœlomic canal enclosed by the ventral arches

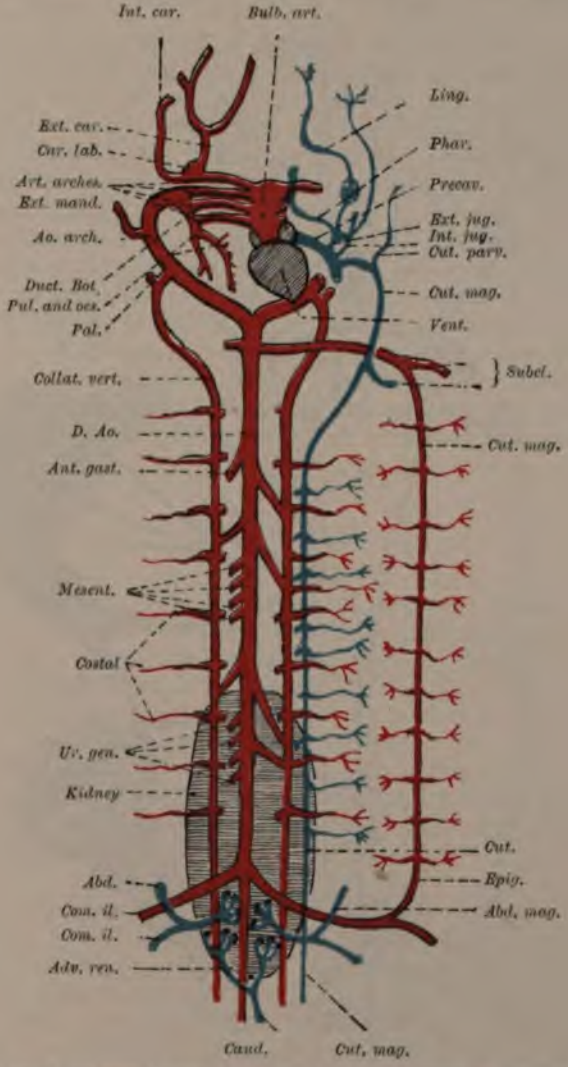

FIG. 322.—DIAGRAM OF THE CHIEF ARTERIES (red) AND CERTAIN OF THE VEINS (blue) OF A URODELE. From the ventral side (modified from Bethgé's figures of the vessels in *Salamandra maculosa* and *Triton tæniatus*).

of the vertebræ; the degree of its development is naturally in correspondence with the size of the tail. In cases where the latter is rudimentary, as in Anthropoids and Man for instance, the

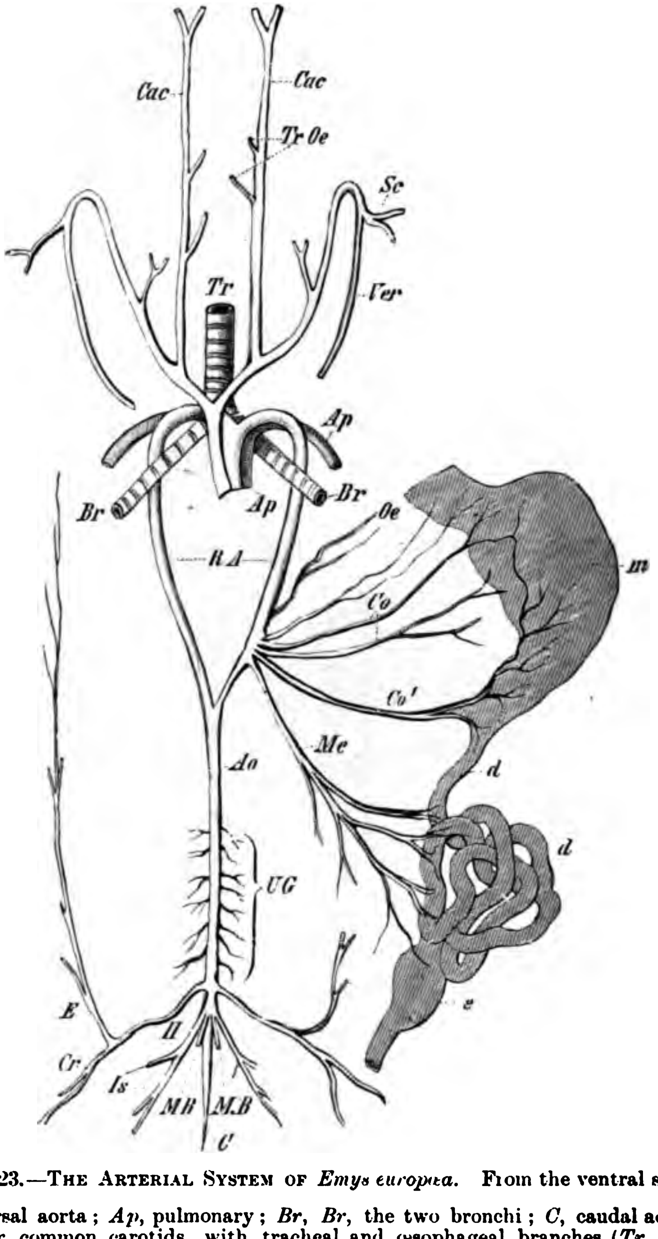

FIG. 323.—THE ARTERIAL SYSTEM OF *Emys europæa*. From the ventral side.

Ao, dorsal aorta; *Ap*, pulmonary; *Br*, *Br*, the two bronchi; *C*, caudal aorta; *Cac*, common carotids, with tracheal and œsophageal branches (*Tr*, *Oe*); *Co*, *Co*^{1}, and *Me*, cœliaco-mesenteric, which here arises as a bundle of separate vessels; *Cr*, femoral; *d*, *d*, small intestine; *E*, epigastric; *e*, large intestine; *Is*, sciatic; *m*, stomach; *MB*, posterior mesenteric; *RA*, aortic arches; *Sc*, subclavian; *Tr*, trachea; *UG*, urinogenital arteries; *Ver*, vertebral.

caudal aorta is spoken of as the *median sacral artery*, and the aorta here appears to be directly continued, not by it, but by the *common iliac arteries*, which pass outwards into the pelvic region (Fig. 322).

Each common iliac artery becomes divided into an *internal iliac*, or *hypogastric*, supplying the viscera of the pelvis and derived from the proximal portion of the embryonic allantoic artery, and an *external iliac*, which is continued into the *femoral* or *crural* and supplies the hinder extremity. In some cases (*e.g.* Sauropsida) the internal and external iliacs come off separately from the aorta (Fig. 323), thus indicating the primary segmental nature of the arteries supplying the embryonic extremity.

The arteries of the hind-limb, like those of the fore-limb, have undergone considerable modifications in the course of phylogeny. Thus it is highly probable that the femoral artery was not originally the chief vessel of the posterior extremity, but that the main flow of blood passed along the sciatic artery arising more posteriorly from the aorta, as is still the case in the Amphibia and Sauropsida and in certain embryonic stages in Mammalia.[1]

VENOUS SYSTEM.

Amphioxus.—The blood from the intestine passes into a *subintestinal vein* which extends forwards as the *hepatic portal vein* to the ventral side of the rudimentary liver, where it divides up into a capillary network (Fig. 324). From this it passes into a *hepatic vein* on the dorsal side of the liver, and this vein becomes continuous with the contractile ventral aorta. A series of segmental veins in the body walls opening into anterior and posterior cardinal veins, comparable to those of Fishes and communicating with the ventral aorta by precaval veins, have also been described (Fig. 324).

Fishes.—Taking the Elasmobranchii more particularly into consideration, a few of the more important facts as regards the development of the veins must first be considered (cf. p. 397).

The first veins to appear in the embryo are the paired *omphalo-mesenteric veins*, which bring back the blood from the surface of the yolk and from the walls of the gut (Figs. 300, 326, I, II). The vessels from the former region are known as *vitelline veins*, while those from the latter give rise to *subintestinal veins* (Fig. 326, III—VII) running beneath the embryonic intestine, which primarily

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[1] The tibialis antica and tibialis postica, like the radial and ulnar arteries of the fore-arm, do not represent the chief vessels of the shank. At an earlier stage all these were relatively small branches, while the main stream passed along an *internal interosseous* and then a *median* artery in the fore-arm, and a *peroneal* or branches of a primitive *saphenous* artery in the shank.

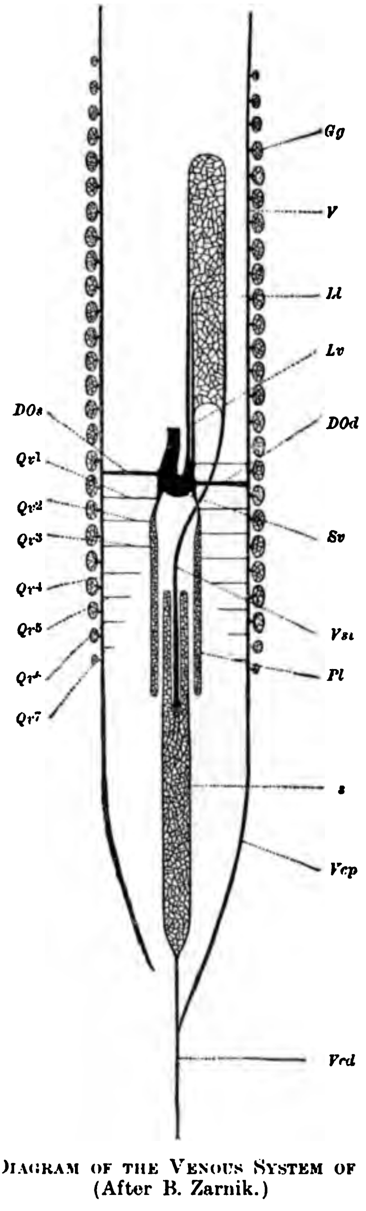

FIG. 324.—DIAGRAM OF THE VENOUS SYSTEM OF *Amphioxus*. (After B. Zarnik.)

DCd, *DCs*, right and left precaval; *Ds*, intestinal sinus; *Gg*, genital vessels; *Ll*, heptic lacunæ; *Lv*, hepatic vein; *Pl*, parietal lacunæ; Qv^1,—Qv^7, transverse veins; *Sv*, vental aorta (" sinus venosus ") ; *Vca*, anterior cardinal; *Vcd*, caudal; *Vcp*, posterior cardinal; *Vsi*, subintestinal vein.

extends into the caudal region as the post-anal gut. On the disappearance of the latter, the posterior part of the subintestinal

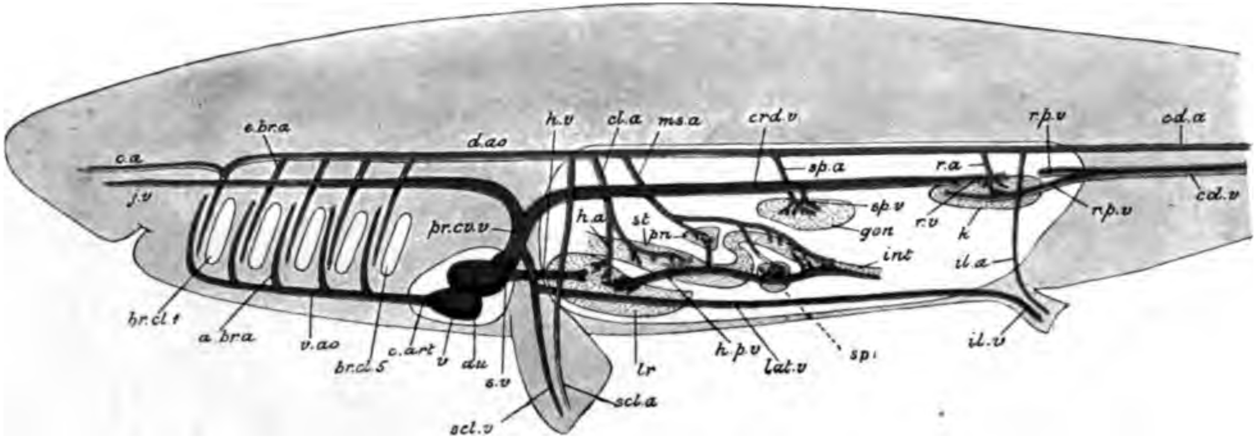

FIG. 325.—SEMIDIAGRAMMATIC SIDE VIEW OF THE VASCULAR SYSTEM OF A DOGFISH. (From T. J. Parker's *Elementary Biology*.)

a.br.a, afferent branchial arteries; *au*, atrium; *c.a*, carotid; *c.art*, truncus arteriosus; *cd.a*, caudal artery; *cl.a*, cœliac artery, supplying the stomach (*st*) and liver (*lr*); *d.ao*, dorsal aorta; *e.br.a*, efferent branchial arteries; *h.a*, hepatic artery; *il.a*, iliac artery; *ms.a*, mesenteric artery, supplying the intestine (*int*), pancreas (*pn*), and spleen (*spl*); *r.a*, renal arteries; *scl.a*, subclavian artery; *sp.a*, spermatic arteries; *s.v*, sinus venosus; *v*, ventricle; *v.ao*, ventral aorta.
cd.v, caudal vein; *crd.v*, posterior cardinal; *j.v*, jugular (anterior cardinal) vein; *pr.cv.v*, precaval; *r.p.v*, renal portal; *r.v*, revehent renal veins; *sp.v*, spermatic veins.
h.p.v, hepatic portal vein; *h.v*, hepatic veins; *il.y*, iliac vein; *lat.v*, lateral vein; *s.clv*, subclavian vein.

vessels gives rise to the *caudal vein*, which now lies directly beneath the caudal aorta and loses its direct connection with the anterior part (VIII—XII). As the liver is gradually developed,

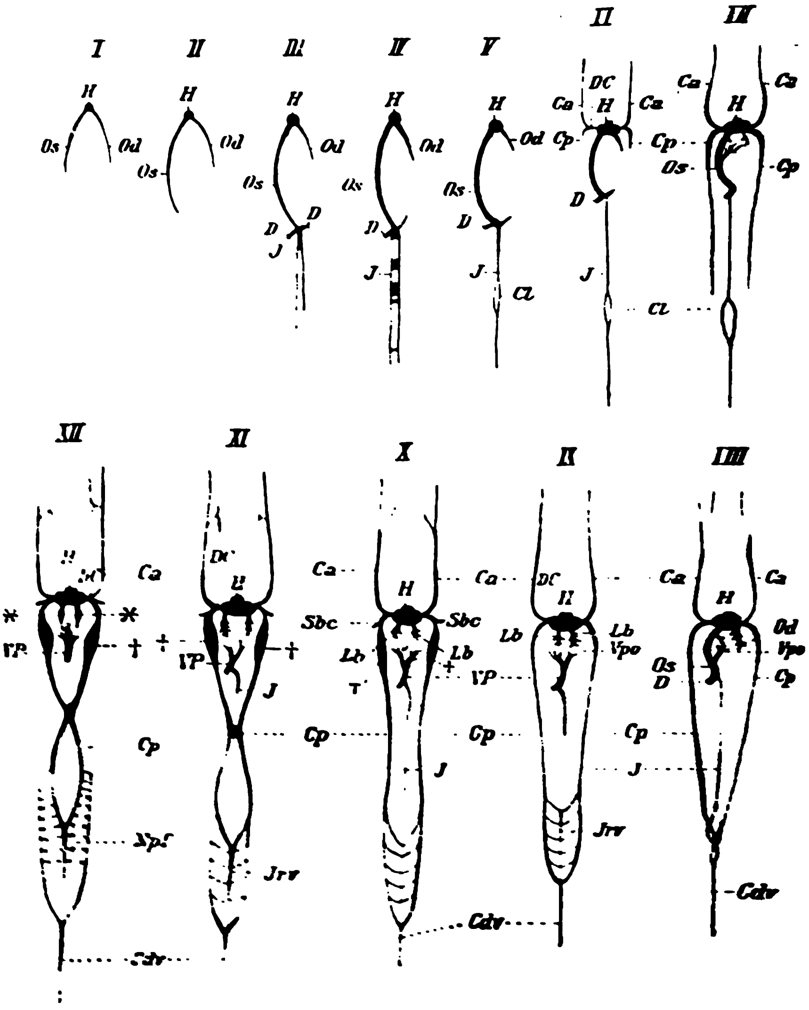

Fig. [illegible].—Diagrams of Stages in the Development of the Veins in Elasmobranchs. I–XI after Rabl, XII after F. Hochstetter.

Ca, *Cp*, anterior and posterior cardinal veins; *Cdv*, caudal vein; *Cl*, region of the cloaca; *DC*, precaval vein or sinus; *D*, *D*, vitelline veins; *H*, sinus venosus of heart; *J*, subintestinal vein; *Jrv*, interrenal vein; *Lb*, hepatic veins; *Npr*, renal portal system; *Os*, *Od*, left and right omphalo-mesenteric veins; *Sbc*, subclavian vein; *VP*, hepatic portal vein; *Vpo*, capillaries of the hepatic portal system; *, hepatic sinus; +, cardinal sinus.

the main trunk of the left omphalo-mesenteric vein breaks up into hepatic capillaries, which again unite anteriorly, opening into the proximal ends of both these veins. The latter thus give rise to

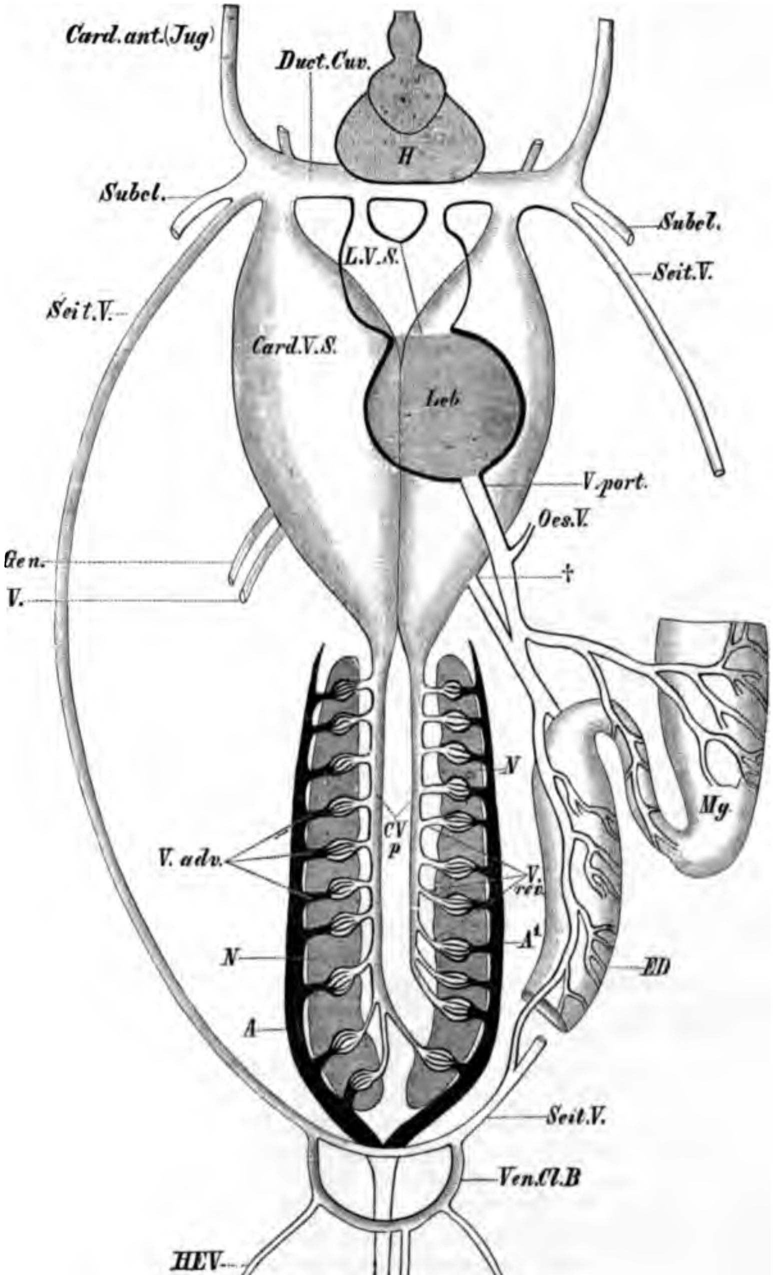

FIG. 327.—For description see next page.

FIG. 327.—DIAGRAM OF THE VEINS OF AN ELASMOBRANCH. **From the ventral side.**

Card.ant.(Jug), anterior cardinal (jugular); the inferior jugular is seen nearer the middle line; _Card. V.S_, cardinal sinus, communicating with its fellow in the middle line; _Caud.v_, caudal vein, which divides into two renal portals, A, A^1, at the posterior end of the kidneys (N): from these arise the advehent veins of the renal portal system (_V.adv_); _Duct.Cuv_, precaval sinus; _Gen. V_, genital veins; _H_, heart; _Leb_, liver; _L.V.S_, hepatic sinus; _Seit. V_, lateral vein, into which open a venous network in the region of the cloaca (_Ven.Cl.B_), one or more cutaneous veins of the tail (_Cut. V_), and veins from the body-walls and pelvic fins (_HEV_); _Subcl_, subclavian; _V.port_, hepatic portal vein, receiving its blood from the intestine (_ED_), stomach (_Mg_), and œsophagus (_Oes. V_), and anastomosing with the lateral vein posteriorly and with the cardinal sinus anteriorly; _V.rev_, revehent renal veins, from which the posterior cardinals (_CV_) arise; †, anastomosis between portal and systemic veins.

the *hepatic veins*, which open into the sinus venosus. New vessels from the various parts of the alimentary canal (gastric, splenic, and mesenteric veins) are gradually developed, the pre-caudal portion of the subintestinal vein becoming of minor importance; all these vessels unite to form what is now known as the *hepatic portal vein*, and thus pour their blood through the capillaries of the liver (Figs. 325–329, and 331).

Anteriorly to the heart, a paired *precaval vein* (*ductus Cuvieri*) is developed, and opens into the sinus venosus. This is formed, on either side, by the confluence of an *anterior* and a *posterior cardinal vein*, the former bringing back the blood from the head (*external* and *internal jugulars*), and the latter from the body, in which it runs on either side of the aorta, between the latter and the kidneys. A paired *inferior jugular* from the ventral part of the head into which the nutrient branchial veins open, also communicates with the precaval. A *subclavian vein* from the pectoral fin also enters to the precaval sinus or proximal end of the posterior cardinal vein.

The caudal vein usually bifurcates posteriorly to the cloaca, each branch passing along the outer side of the corresponding kidney, and giving off advehent vessels into the latter. These divide up into capillaries, forming a *renal portal system*, the capillaries again uniting to form revehent veins which open into the posterior cardinals. Thus the condition of the veins typical of adult Fishes is reached, and a few of the more important modifications must now be briefly referred to.

In Cyclostomes, Elasmobranchs, and Dipnoans, the anterior part of the subintestinal vein still persists as a small vessel running within the spiral valve of the intestine. In the Elasmobranchs, many of the veins (*e.g.*, precavals, anterior and posterior cardinals, inferior jugulars, hepatic and genital veins) enlarge to form capacious *sinuses*, and a large *lateral vein* (Figs. 325, 327), running in the body-walls, opens into each precaval or posterior cardinal. This probably corresponds to the vein of the primary lateral-fin folds (p. 137).

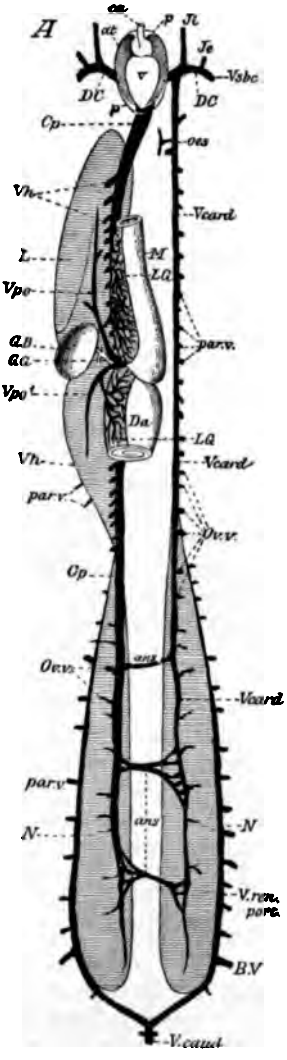

FIG. 328.—DIAGRAM OF THE VENOUS SYSTEM OF *Protopterus annectens.* From the ventral side. (After W. N. Parker.)

at, atrium ; *B.V.* pelvic vein ; *ca*, conus arteriosus ; *Cp*, postcaval ; *Da*, intestine ; *DC*, *DC*, precaval veins ; *G.B*, gall-bladder ; *G.G*, bile-duct ; *Je*, *Ji*, internal and external jugular ; *L*, liver ; *L.G*, lymphoid organ in the walls of the stomach, the blood from which passes into the hepatic portal veins (*Vpo*, *Vpo*¹) ; *M*, stomach ; *N*, *N*, kidneys ; *œs*, œsophageal vein ; *Ov.v*, ovarian veins ; *p*, pericardium ; *par.v*, parietal veins from the body-walls ; *v*, ventricle ; *V.card*, left posterior cardinal vein, which is connected by anastomoses (*ans*) with the postcaval (*Cp*) in the region of the kidneys ; *V.caud*, caudal vein ; *Vh*, *Vh*, hepatic veins ; *V.ren.port*, renal portal vein ; *Vsbc*, subclavian.

A renal portal system is absent in Cyclostomes and certain Elasmobranchs, and is inconstant and very variable amongst Teleostomes: in many instances the caudal vein communicates directly with one or with both posterior cardinals, and in the former case the other cardinal shows a tendency to become reduced in size: a similar reduction occurs in many of the forms described below.

The chief point of interest as regards the veins of Dipnoans (Fig. 328) is the presence of a large unpaired *postcaval vein*, derived in part from the posterior cardinal, and comparable to that of the Amphibia and Amniota. A renal portal system is present, and the blood from the kidneys is collected into two veins having the relations of posterior cardinals. Only the left of these, however, opens anteriorly into the corresponding precaval, the right, which is much the larger of the two, passing along the dorsal border of the liver to open independently into the sinus venosus in the middle line. The renal portion of this vein is evidently homologous with the corresponding part of the posterior cardinal, the anterior portion of which can no longer be recognised. Thus the postcaval is made up of a posterior or renal portion, and of an independently developed anterior or hepatic portion.

In Ceratodus the posterior cardinal and postcaval are directly continuous with the caudal vein, and the renal portal, receiving branches from the posterior end of the body, arises from the iliac vein, which also gives off a pelvic branch. The latter unites with its fellow in the middle line to form a median *abdominal vein*, comparable to that of the Amphibia (cf. Fig. 329) and opening into the sinus venosus. Afferent renal veins also enter the postcaval and cardinal, the corresponding efferent vessels opening into the left cardinal and caudal veins; the renal portal system is thus more complicated than in other Dipnoans. The two pulmonary veins unite into a single trunk before opening into the left atrium.

Amphibians.—A large postcaval vein arises in essentially the same manner as in the Dipnoi, its renal section being formed by the fusion of the two posterior cardinals in this region. The hepatic portion apparently arises in part from the right omphalo-mesenteric vein, and in part independently, while the hepatic portal vein is developed from the left omphalo-mesenteric. The postcaval receives blood from the kidneys and generative organs, as well as indirectly from the posterior extremities, body-walls, and tail (when present). The anterior part of both posterior cardinals persists in Urodeles and in Bombinator as the paired *azygos vein*, and this may exceptionally be present on one or both sides in other Anurans. It communicates with the corresponding precaval (Fig. 329).

A renal portal system is present, and is formed, as in Fishes, by the bifurcation of the caudal vein, which is wanting in adult

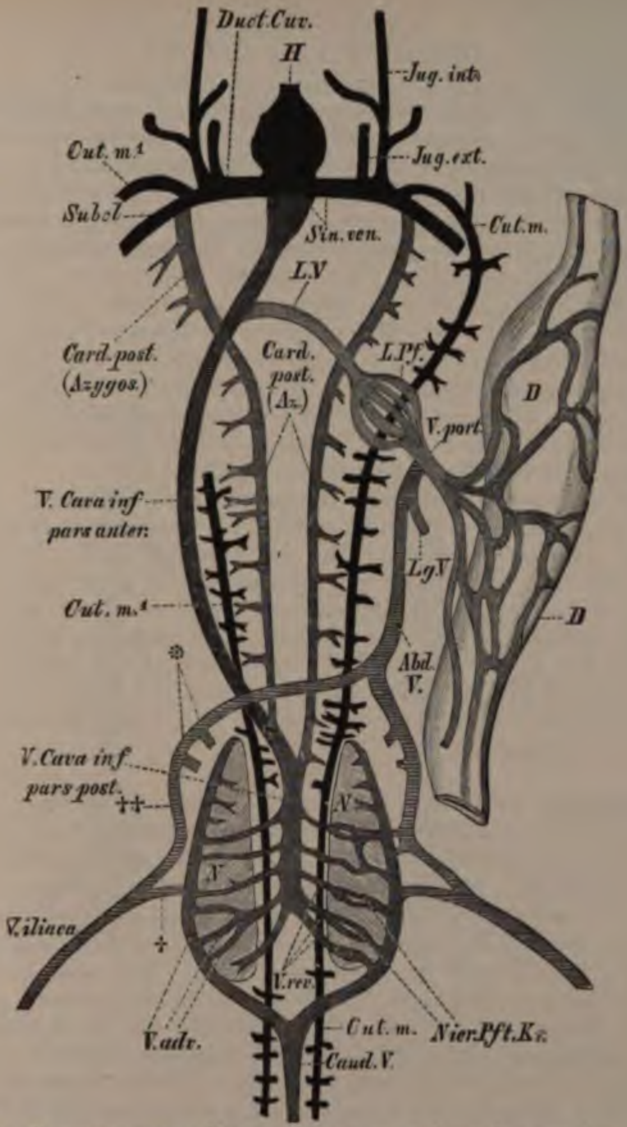

FIG. 329.—DIAGRAM OF THE VENOUS SYSTEM OF *Salamandra maculosa*. From the ventral side.

Card.post (*Azygos*), posterior cardinal or azygos; *Caud. V*, caudal vein, which bifurcates at the posterior end of the kidneys (*N*, *N*) to form the renal portal system (*Nier.Pft.Kr*); *Cut.m*, left great cutaneous (musculo-cutaneous) vein; *Cut.m*¹, the same on the right side (partly removed); *Duct.Cuv*, precaval; *D*, *D*, alimentary canal, from which the hepatic portal vein (*V.port*) arises; *H*, heart; *Jug. ext.* and *Jug. int.* external and internal jugulars; *Lg.V*, longitudinal vein of the intestine: *L.Pf*, hepatic portal system; *LV*, hepatic vein; *Subcl*, subclavian vein; *V.adv*, *V.rev*, advehent and revehent renal veins; *V.Cava inf. pars anter*, and *V.Cava inf. pars. post*, anterior and posterior sections of the postcaval; *V.iliaca*, femoral vein, which divides into an anterior (††) and a posterior (†) branch: the latter opens into the renal portal, and the former (pelvic vein) [illegible] w to form the abdominal vein (*Abd.V*), and also [illegible] om the cloaca, bladder, and posterior part of the int[illegible]

Anura; into the renal portal open the veins from the hind-limb, and vessels from the body-wall often also communicate with it. The blood from the kidneys passes into the postcaval. Connecting the right and left renal portals (or femorals) is a transverse *pelvic vein*, from which, in the medio-ventral line of the body, an *abdominal* or *epigastric vein* arises, as in Ceratodus: this is primitively paired, and its paired condition may even be retained in the adult posteriorly (cf. Fig. 322); it corresponds genetically to the lateral veins of Elasmobranchs. This vein extends forwards in the ventral body-wall into the liver, in which it breaks up into capillaries, becoming secondarily connected by anastomosis with the hepatic portal vein. The abdominal vein receives blood from the cloaca, bladder, and body-walls. In Urodeles remains of the subintestinal vein also open into the hepatic portal system.

The arrangement of the anterior cardinals (external and internal jugulars) is essentially similar to that seen in Fishes.

The venous blood from the integument of the body and frequently that of the tail also, passes into a *great cutaneous* or *musculo-cutaneous vein*, which extends forwards along the longitudinal muscles of the trunk, and then makes a wide curve towards the fore-limb, where it unites with the subclavian vein (Figs. 322 and 329). Shortly before opening into the sinus venosus the combined trunk receives a small vein from the laryngeal mucous membrane.

Amniota.—The section of the right posterior cardinal vein in the region of the embryonic kidney (mesonephros) gives rise to the hinder part of the postcaval: the hepatic section of the latter arises as in Amphibia. In the Sauropsida the anterior portions of both posterior cardinals disappear to a greater or less extent, and are replaced by *vertebral veins*, while in Mammals they may persist and may form part of the *azygos veins*. An anastomosis is formed between these latter, and eventually the anterior part of the left disappears more or less completely, the blood from both sides passing into the right azygos (hemiazygos), which opens into the right precaval (Figs. 330 and 331). As the azygos and postcaval both receive part of their blood from the lumbar and pelvic regions, the former forms an important communicating channel between the latter and the precaval.

The anterior cardinal gives rise, as in lower Vertebrates, to the jugular, which, as well as the subclavian and vertebral or azygos, opens into the precavals. In Reptiles, Birds, Monotremes, and Marsupials, as well as in many Rodents, Insectivores, Bats, and Ungulates, both precavals persist throughout life; in other Mammals the main part of the left disappears, all the blood from the head and anterior extremities passing into the right precaval. The coronary veins open into the base of the left precaval (coronary sinus, Fig. 317).

A renal portal system occurs in connection with the embryonic kidney in all Sauropsida, and traces of it can also be recognised in Mammalian embryos, being particularly well seen in those of Echidna. In adult Reptiles and Birds other connections of the vessels are set up, so that only indications of the renal portal system are usually retained, and in Mammals are entirely wanting.

As in Fishes, the first veins to appear in the embryo are the vitelline or omphalo-mesenteric veins (Fig. 331, A), bringing back the blood from the yolk-sac, and uniting into a single trunk before opening into the sinus venosus. As the liver becomes developed it surrounds this trunk, which sends advehent branches into it, revehent branches returning the blood into the anterior section and eventually giving rise to a right and a left hepatic vein. Thus a portal circulation arises, and the main trunk of the vein,

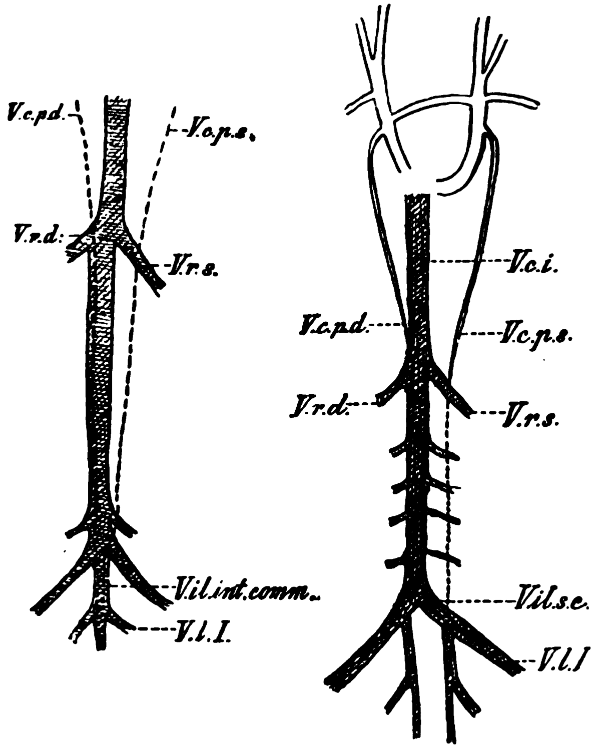

FIG. 330.—DIAGRAM SHOWING THE RELATIONS OF THE POSTERIOR CARDINAL AND POSTCAVAL VEINS IN A, THE RABBIT, AND B, MAN. (After Hochstetter.)

V.c.i, postcaval; *V.c.p.d*, *V.c p.s*, right and left posterior cardinals; *V.il.int.comm*, common internal iliac vein; *V.il.s.c*, common iliac vein; *V.l.l*, lumbar vein; *V.r.d*, *V.r.s*, renal veins.

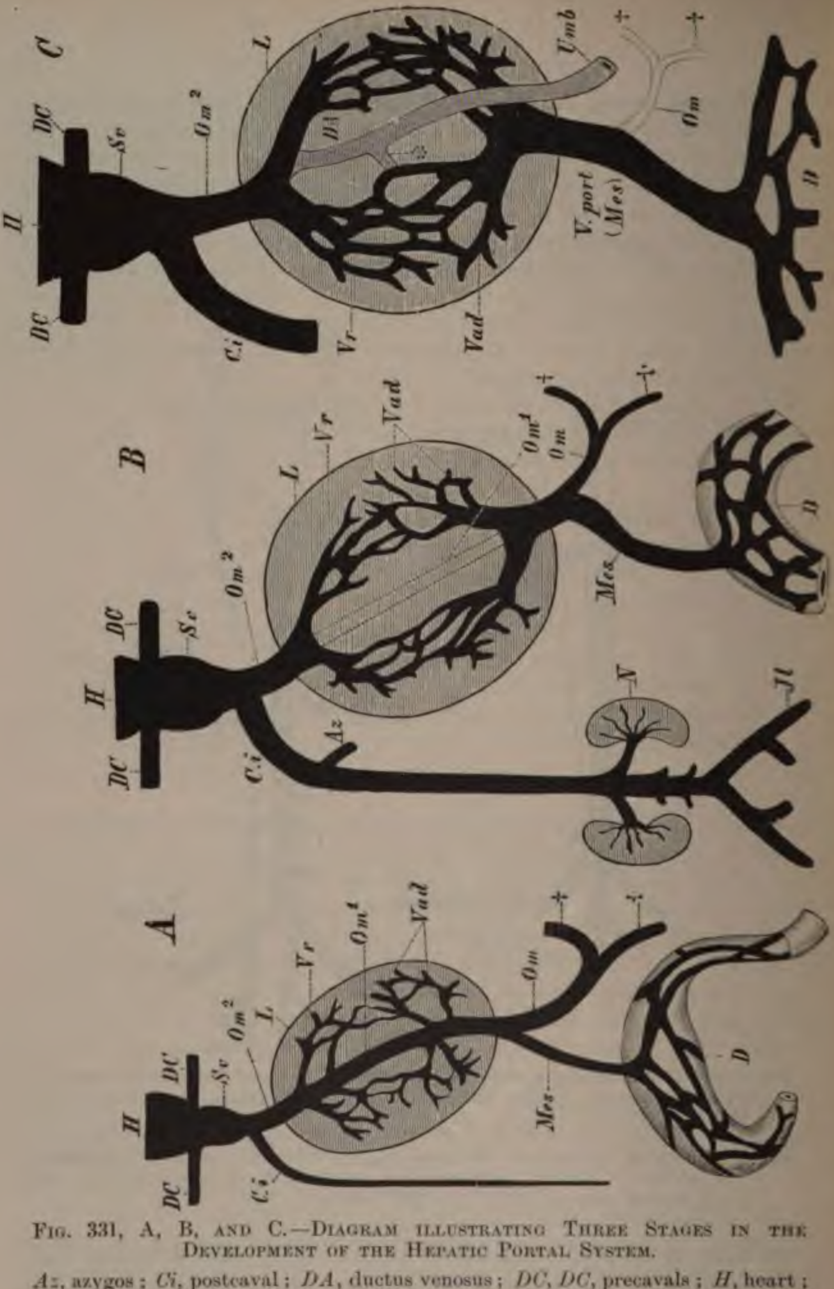

FIG. 331, A, B, AND C.—DIAGRAM ILLUSTRATING THREE STAGES IN THE DEVELOPMENT OF THE HEPATIC PORTAL SYSTEM.

Az, azygos ; *Ci*, postcaval ; *DA*, ductus venosus ; *DC*, *DC*, precavals ; *H*, heart ; *Il*, iliac vein ; *L*, liver ; *Mes*, mesenteric vein, which later gives rise to the hepatic portal (*V.port*), receiving blood from the alimentary canal (*Mes*, *D*) ; *N*, kidney ; *Om*, Om^1, Om^2, the three sections of the vitelline or omphalomesenteric vein (the first still shows its originally paired nature at †† : in stage *B*, the second section of this vein which passes through the liver, disappears, so that *Om* and Om^2 are only connected by capillaries : in stage *C*, the first section (*Om*) has quite disappeared, and the umbilical vein (*Umb*) has become developed ; *Sv*, sinus venosus ; *Vad*. advehent veins ; *Vr*, revehent veins ; *, connection of the umbilical vein with the capillaries of the liver.

where it passes through the liver, gradually disappears. In the meantime, the cœliac and mesenteric veins have appeared, and all the blood from them, as well as from the vitelline veins, now passes through a common trunk, the hepatic portal vein, into the capillaries of the liver, whence it reaches the sinus venosus through the hepatic veins. The portions of the vitelline veins posterior to the liver also gradually disappear as the yolk-sac becomes reduced.

In addition to these vessels, the *umbilical vein* must also be mentioned. This vessel also is originally paired, and corresponds phylogenetically to the lateral veins of Elasmobranchs and to the abdominal or epigastric vein of Ceratodus and Amphibians. It is situated originally in the body-walls, and comes into relation with the allantois (p. 9), opening primarily into the sinus venosus and eventually into the postcaval: as the allantois increases in size it brings back the oxygenated blood from this organ (*i.e.*, from the placenta in the higher Mammalia) to the embryo. The right umbilical vein, however, is early obliterated, and the left comes into connection with the capillaries of the liver, its main stem in this region disappearing (Fig. 331, B); thus the blood from the allantois has to pass through the capillaries of the liver before reaching the heart. In the course of development, however, a direct communication is formed between the left umbilical vein and the revehent branches of the fused vitelline veins, and this trunk is known as the *ductus venosus* (Fig. 331, C): the point at which it opens corresponds to that from which the postcaval has in the meantime arisen, the hepatic veins now appearing as factors of the latter. On the cessation of the allantoic (or placental) circulation, the ductus venosus becomes degenerated into a fibrous cord, so that all the portal blood has to pass through the capillaries of the liver.

The intra-abdominal portion of the umbilical vein persists throughout life as the epigastric vein in Reptiles and in Echidna, but disappears in Birds and in other Mammals.[1]

Retia Mirabilia.

By this term is understood the sudden breaking-up of an arterial or venous vessel into a cluster of fine branches, which, by anastomosing with one another, give rise to a capillary network; the elements of this network may again unite to form a single vessel. The former condition may be described as a *unipolar*, the latter as a *bipolar* rete mirabile. If it is made up of arteries or of veins only, it is called a *rete mirabile simplex*; if of a combination of both kinds of vessels, it is known as a *rete mirabile duplex*.

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[1] The mode of development of the veins of the extremities is essentially similar in all the Amniota, and at first resembles that occurring in Urodela, though later on considerable differences are seen, more especially as regards the veins of the digits.

The retia mirabilia serve to retard the flow of blood, and thus cause a change in the conditions of diffusion. They are extremely numerous throughout the Vertebrate series, and are found in the most varied regions of the body, as, for instance, in the kidneys (glomeruli)—where their above-mentioned function is most clearly seen; on the ophthalmic branches of the internal carotid; on the pseudobranchs and on the vessels of the swim-bladder in Fishes; on the portal vein; and along the caudal portion of the vertebral column in Lizards. In Mammals, they are best developed in Edentates, but occur also in Cetacea, Pinnipedia, Rodents, Marsupials, Lemurs, &c.

LYMPHATIC SYSTEM.

The lymphatic system consists of branched *lymph-vessels*, situated in the connective tissue of various parts of the body, and of *lymph-sinuses*: it serves to collect the blood-plasma which has passed through the walls of the capillaries and to pass it into the veins. The lymph, as already mentioned, contains leucocytes.

It is probable that in all Craniates the lymphatic system is primarily paired and symmetrical: the first trunks which appear in the embryo have apparently a similar course to that of the main veins. Thus paired vessels (*cephalic ducts*) extend backwards from the head, and others (*thoracic ducts*) forwards along the trunk in similar positions to the anterior and posterior cardinal veins respectively. On either side the cephalic and thoracic ducts unite and open into a vein in the region of the precaval. In the course of development, however, anastomoses are formed between the trunk of either side: thus portions of the main trunks may become of minor importance and undergo reduction, so that asymmetry results, as is sometimes also the case in the venous system. Lymph-vessels are usually abundant in various parts (*e.g.* under the skin, on the alimentary canal) and may form complicated networks.

In Fishes, the lymph-vessels are in many respects not so plainly differentiated from the venous system as in higher forms; a lymph-sinus connected with a vein occurs on either side in the scapular region, and into it lymphatic trunks from the head and body open.[1] A large vessel extends along the spinal canal, and a subvertebral lymph-sinus surrounds the aorta and communicates with others in the mesentery which receive the vessels from the abdominal viscera. Lymphatics are also present on the walls of the heart and great blood-vessels, forming perivascular sheaths.

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[1] The lacunar spaces in Cyclostomes, generally regarded as belonging to the lymphatic system, have been found to contain blood.

In Urodeles, the single thoracic duct bifurcates near the heart, thus indicating its primarily paired character; it receives lymph-vessels from the head, and each branch opens into the corresponding subclavian vein. The arrangement of the lymphatics in Urodeles, and still more in Anurans, becomes considerably modified owing to the presence of *lymph-hearts* and of large sinuses under the skin which communicate with those of the peritoneal cavity (*e.g.* subvertebral, periœsophageal): the cephalic and thoracic ducts disappear, and the only trunks which remain are those connecting the lymph-hearts with the sinuses. Valves occur in the lymphatics where they communicate with the lymph-hearts, sinuses, and veins.

In Reptiles there are two cephalic ducts which open into the subclavian vein along with the thoracic duct, which is either paired (Snakes, Chelonians, Crocodiles), or single, bifurcating anteriorly.

Lymphatic vessels are less developed in Birds than in Mammals: two thoracic ducts arise in the region between the thyroid gland and cœliac artery, having close relations to the aorta and precavals, with the latter of which they communicate at various points: their connection with the longitudinal channels along the posterior part of the aorta takes place later (Fig. 332). As in Reptiles, valves are not abundant, and occur in only a few of the vessels.

In Mammals both thoracic ducts may persist, or that of one side may disappear. Thus in Man the duct is unpaired and usually arises from a sinus (*cisterna* or *receptaculum chyli*) in the lumbar region: it receives the lymphatics from the legs and pelvic organs as well as those from the intestine (*lacteals*) and opens anteriorly into the left brachiocephalic vein, with which also communicate lymph-vessels from the head, neck, and right side of the thorax. The lymphatics, like the veins, are provided with numerous valves in Mammals.

Rhythmically contractile *lymph-hearts* (of which little is known in Fishes except that two are present, *e.g.*, in the caudal region in Silurus and one in the Eel), occur in Amphibians, Reptiles, and embryos of Birds (Fig. 332): they are surrounded by striped muscle. In Urodeles there are as many as 14–20 on either side of the trunk and tail under the skin at the junction of the dorsal and ventral trunk-muscles,[1] while in Anura the number is reduced to two pairs with numerous valves, the anterior of which is situated between the transverse processes of the third and fourth vertebræ and the posterior between the urostyle and pelvis. In Reptiles posterior lymph-hearts only are present, situated at the junction of trunk and tail on the transverse processes or ribs. In Bird embryos they occur at the boundary between the sacral and coccy-

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[1] In the walls of the truncus arteriosus of Urodeles a lymph-sinus is included, which has been described as the "c[illegible]"

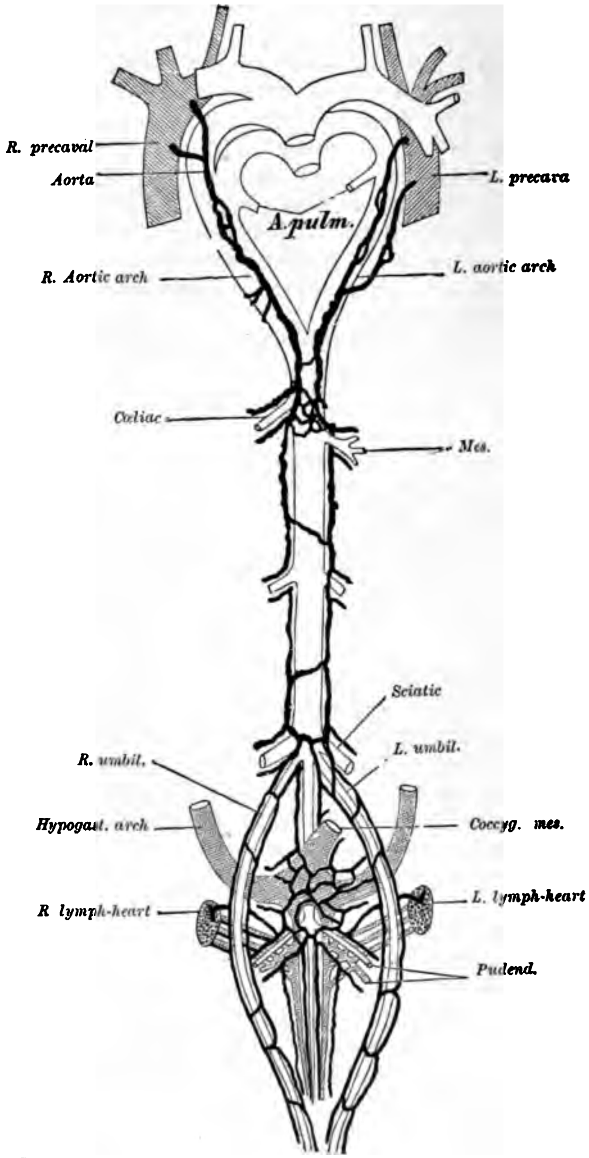

FIG. 332.—DIAGRAM OF THE TWO THORACIC DUCTS AND GREAT ABDOMINAL AND CAUDAL LYMPH-TRUNKS OF A CHICK OF 17 DAYS' INCUBATION. (After L. Sala.)

The arteries are left clear, the veins shaded, the lymphatics black, and the lymph-hearts dotted.

geal vertebræ partly covered by the coccygeus dorsalis muscle: they communicate with the coccygeal and pelvic veins.

Aggregations of leucocytes giving rise to follicles are present in the *lymphoid* or *adenoid tissue* which occurs beneath the mucous membrane in various parts of the body (*e.g.* tonsils, alimentary canal, bronchi, conjunctiva, urinogenital organs): these cells, owing to their power of amœboid movement, have a tendency to wander through the mucous membrane to the surface, and thus doubtless to remove useless and harmful material (*e.g.* broken down particles, inflammatory products, Bacteria): in some cases such leucocytes (*phagocytes*), instead of passing out from the surface, possibly serve to carry material from one part of the body to another.

Lymphoid tissue is very abundant in the body-cavity of Fishes and Amphibians: it occurs in the alimentary canal and round the blood-vessels, but is especially abundant in the neighbourhood of the urinogenital organs. To the same category belong the so-called "fat-bodies" (*corpora adiposa*) of Amphibia and Reptilia, as well as the mass of lymphoid tissue on the heart of the Sturgeon and possibly also the "hibernating glands" of certain Rodents and Insectivores.

The agglomeration of a number of lymphoid follicles gives rise to those structures which are known as "*lymphatic glands*" and as "*hæmolymph*" or "*blood-glands,*" which, in spite of certain characteristic differences, have much in common as regards the structure of their enclosing capsules and of the network of connective tissue-trabeculæ extending through them, and various intermediate forms occur.[1] The *spleen* belongs to the same category as these, and is in a sense intermediate in structure between the more primitive hæmolymph gland and the more highly differentiated lymphatic gland, the three forming an almost continuous series. In the last-mentioned the lymph, and in the two former the blood, passes into a non-tubular network, where it becomes filtered; the worn-out red corpuscles are thus retained and become taken up and digested by the lining epithelial cells and the leucocytes in the process of phagocytosis. All three of these organs, moreover, like the bone-marrow, have the common function of giving rise to new lymph-corpuscles. The spleen, which is present in all or almost all Vertebrates (? Cyclostomes), arises in the region of the mesentery, and has usually close topographical relations to the pancreas: it corresponds to a specially differentiated portion of a tract of lymphoid tissue primarily extending all along the alimentary canal, and in Protopterus still remains enclosed within the walls of the stomach (Fig. 247). In most other Vertebrates it is situated outside the walls of the canal, but even then may extend along the greater part of the latter (*e.g.* Siren). In some cases, however, either the proximal or the distal portion of it undergoes reduction, or only the middle part persists

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[1] Lymphatic glands are most numerous in Mammals, and occur along the lymph-trunks; hæmolymph glands have been found in numerous Mammals and in certain Birds and Fishes.

(Hatteria): thus it is often situated near the stomach, but may be met with in other regions of the intestinal tract, as, for instance, at the commencement of the rectum (Anura, Chelonia). In some cases (*e.g.* Sharks) it is broken up into several portions, and frequently a larger "main spleen" and several smaller "accessory spleens" can be recognised.

The structures known as *tonsils* are most highly developed in Mammals, in which they give rise to a paired organ lying on either side of the fauces—that is, in the region where the mouth passes into the pharynx, and usually also to a mass situated more posteriorly on the walls of the pharynx itself (pharyngeal tonsils); the latter are phylogenetically the older organs and are present in Reptiles, Birds, and most Mammals, and tonsil-like organs also occur in Amphibians on the roof and floor of the oral cavity. The tonsils consist of a retiform (adenoid) connective tissue ground-substance enclosing a number of lymph-corpuscles, which are arranged in so-called follicles.

MODIFICATIONS FOR THE INTRA-UTERINE NUTRITION OF THE EMBRYO: FŒTAL MEMBRANES.

I. ANAMNIA.

IN several **Elasmobranchs** the oviduct gives rise to glandular villi which secrete a nutritive fluid, and in an Indian Ray (Pteroplatea micrura) there are specially long glandular villiform processes which extend in branches through the spiracles into the pharynx of the embryos, of which there may be as many as three in each oviduct. In certain viviparous Sharks (viz., Mustelus lævis and Carcharias) the walls of the vascular yolk-sac become raised into folds or villi, which fit into corresponding depressions in the walls of the oviduct, the latter becoming very vascular. A kind of *umbilical placenta* is thus formed, by means of which an interchange of nutritive, respiratory, and excretory matters can take place between the maternal and fœtal blood-vessels.

Amongst viviparous **Teleosts** various arrangements for the nutrition of the embryo occur. In Zoarces viviparus and in the Embiotocideæ the embryos are retained in the hollow ovary, the empty follicles (corpora lutea) of which give rise to extremely vascular villi, from which a serous fluid containing blood- and lymph-cells is extruded into the cavity of the ovary and thus surrounds the masses of embryos: these swallow the fluid and digest the contained cells. In other forms (*e.g.* viviparous Blennies and Cyprinodonts), the embryos undergo development within the vascular ovarian follicles, and are probably nourished by diffusion; in Anableps, villi are developed from the yolk-sac, and these doubtless absorb the nutritive fluid from the walls of the ovary.

In certain **Amphibians** which have no free larval existence, interesting modifications occur for nourishing the young until the larval stage is passed. Thus in the Alpine Salamander (Salamandra atra), a large number of ova (40—60) pass into each oviduct, just as in the allied S. maculosa, in which the young are born as gilled larvæ. Were this the case in S. atra, the young would be carried away in the mountain streams and destroyed, and a curious adaptive modification has arisen in this form, in which only one embryo (that nearest the cloaca) in each oviduct undergoes complete development, remaining within the body of the parent until the gills are lost and complete metamorphosis has taken place. The other eggs break down and form a food-mass for the survivors after their own yolk is used up. Degenerative changes, moreover, take place in the epithelium of the oviduct, and masses of red blood-corpuscles pass into the lumen of the latter, undergo degeneration, and become mixed with the broken-down yolk-masses, the resulting broth being swallowed by the surviving young. The long, feather-like external gills are closely applied to the uterine mucous membrane, and so effect an interchange of gases in respiration. After the young is born, the uterine epithelium becomes regenerated, and thus a process occurs which somewhat resembles that of the formation of a *decidua* in placental Mammals.

II. AMNIOTA.

In all the Amniota, as already mentioned (p. 9), fœtal membranes, known as the *amnion* and *allantois* are developed, and the latter, or primary urinary bladder, represented only in rudiment in the Amphibia, is of great importance in connection with respiration, excretion, and (in the higher Mammals) nutrition in the embryo.

A glance at Fig. 8 will show that owing to its mode of development, the amnion[1] consists primarily of two layers; an inner, the *amnion proper*, and an outer or *false amnion*. The latter comes to lie close to the vitelline membrane, and forms the so-called *serosa*, or *serous membrane*. As the allantois grows, it extends into the space continuous with the cœlome between the true and false amnion, and may entirely surround the embryo.

Amongst **Reptiles,** the eggs of the viviparous Lizard, Seps chalcides, are relatively poor in yolk, and this is compensated for by the yolk-sac and allantois coming into close relation with the walls of the oviduct, thus forming an *umbilical* and an *allantoic placenta*, one at each pole of the embryo; the latter of these is the more important. Both fœtal and maternal parts of the placenta become extremely vascular, and thus the necessary interchange of materials can take place between the blood of the embryo and mother. In Trachydosaurus and Cyclodus, as well as in the Chelonia, a kind of umbilical placenta is apparently also formed.

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[1] As the head enlarges and sinks downwards, it is at first surrounded by a modification of the head fold (p. 9) consisting entirely of ectoderm and called the *proamnion*: this is afterwards replaced by the true amnion.

The fact that a vascular yolk-sac (often known as the *umbilical vesicle*) is present in all **Mammals,** indicates that they are descended from forms in which, as in the Sauropsida, the eggs were rich in yolk, and which were viviparous. This condition is moreover retained in the Monotremes, and even in Marsupials the ova are relatively large as compared with those of the higher Mammalia.

As the amount of yolk was gradually reduced in the course of phylogenetic development, close relations were set up between the fœtal (allantoic) and maternal blood-vessels, the allantois becoming closely applied to the serosa to form a *chorion* (Fig. 333); but that this condition was only very slowly evolved is shown by the fact that, even at the present day, Mammals exist in which it has not been reached. These (viz., Monotremes and most Marsupials) are therefore known as *Aplacentalia* or *Achoria*, in contradistinction to the higher *Placentalia* or *Choriata*. Moreover, in the Rodentia, Insectivora, Cheiroptera, Carnivora, and Ungulata more or less distinct indications of an *umbilical placenta*, formed in connection with the yolk-sac, can still be observed, and at a still earlier stage the ova are nourished by the uterine lymph.

In Monotremes and Marsupials, both the yolk-sac and allantois take part in respiration; in the former the two are of equal importance, while amongst the latter the yolk-sac is solely (*e.g.* Dasyurus) or mainly (*e.g.* Phalcolarctos) important in this respect. In Perameles obesula a further approach towards the formation of a true allantoic placenta is seen, the allantois giving rise to small vascular villi. In most Marsupials the allantois serves merely as a urinary reservoir, and in none of them does it possess any important function as an organ of nutrition, the young being born at a relatively early stage, when they become attached to the teats of the mother, and are then nourished by means of milk (cf. p. 375): the form of the mouth and also that of the teats is especially adapted to this end.

In the higher Mammals, the umbilical placenta has usually only a very temporary importance, though in some cases (*e.g.* Rodents) it probably takes some part in respiration and nutrition during the whole uterine life. The allantois extends out from the body of the embryo and becomes attached to the serous membrane to form the chorion, from which numerous villi extend into the uterine wall (Fig. 333). As both the latter and the allantois become extremely vascular, the uterine and allantoic capillaries and sinuses coming into close contact with one another, a complicated allantoic placenta arises, consisting of maternal and fœtal parts

(Fig. 9). Thus the embryo is supplied by diffusion with the necessities for existence during its comparatively long intra-uterine life.

Various forms of placenta are met with amongst the Placentalia. The most primitive type is apparently that in which the allantois becomes attached around the whole serosa, so that the resulting chorion, from which the comparatively simple villi arise, are equally distributed over the whole surface (Fig. 333). This form is known as a *diffuse placenta*, and is met with in Manis, the Suidæ, Hippopotamus, Tylopoda, Tragulidæ, Perissodactyla, and Cetacea.

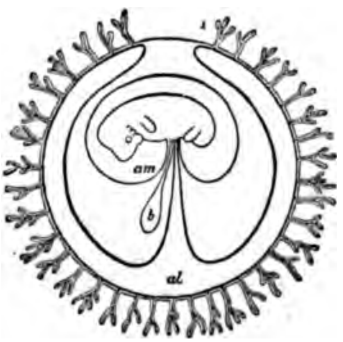

Fig. 333.—Diagram of the Fœtal Membranes of a Placental Mammal. (From Boas's *Zoology*.)

al, allantois; *am*, amnion; *b*, yolk-sac (umbilical vesicle); the outermost line represents the serous membrane. The outer wall of the allantois has united with the serous membrane to form the chorion from which villi arise.

The next stage is characterised by the chorionic villi becoming more richly branched so as to present a greater superficial extent, and at the same time concentrated into definite and more or less numerous patches or cotyledons. Thus a *polycotyledonary* placenta arises, such as is met with in most Ruminants, some of which, such as Cervus mexicanus and the Giraffe, show an interesting intermediate form of placenta between the diffuse and the cotyledonary.

The chorionic villi in these two types of placenta, even when branched, separate from the uterine mucous membrane at birth, the latter not becoming torn away; they are therefore spoken of as *non-deciduate.*

A further complication is seen in the forms of placenta known as *zonary*, the *dome-* or *bell-shaped*, and the *discoidal*, in which the connection between fœtal and maternal parts becomes much more close, the villi giving rise to a complicated system of branches within the uterine mucous membrane (Fig. 334). Thus the latter becomes to a greater or less extent torn away at birth, forming a *decidua*, the placenta being therefore spoken of as *deciduate.* In these cases, the placental part of the chorion does not extend all round the embryo. In the zonary placenta only the two opposite poles of the chorion are more or less free from vascular villi, and this girdle-like form occurs in the Carnivora, as well as in the Elephant, Hyrax, Orycteropus, and Halicore. In Lemurs and Sloths, the placenta is dome- or bell-shaped, while in Myrmecophaga, Dasypodidæ (Armadilloes), and Primates (Fig. 9) it forms a discoidal mass on the dorsal side of the embryo. In Rodentia, Insectivora, and Cheiroptera, though the placenta is also discoidal, it has probably not arisen, like that just mentioned (metadiscoidal form) from a diffuse type, but was originally restricted to a discoidal area, owing to the umbilical vesicle occupying a large surface of the chorion.[1]

From the above description it is evident that the differences in the form of the placenta are mainly those of degree, and that the placenta gives little indication of the systematic position of the animal in question.

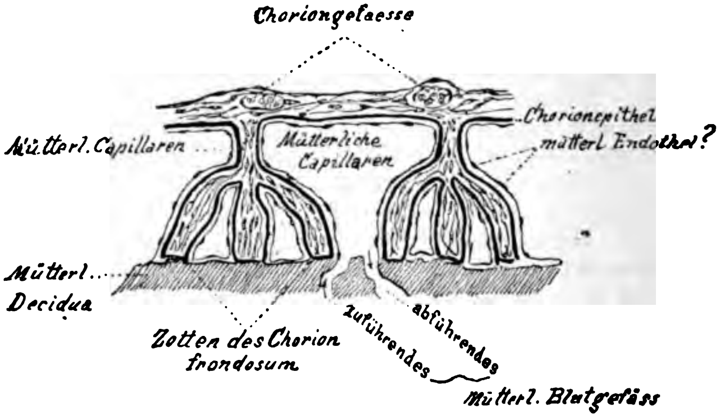

Fig. 334.—Diagram to illustrate the Relations of the Fœtal and Maternal Vessels in the Human Placenta, showing Chorionic and Maternal Vessels (*Gefässe*) and Capillaries, Villi (*Zotten*), and Decidua. (After Keibel.)

In the course of development the embryo becomes more and more folded off from the yolk-sac (Fig. 8), the stalk of which and that of the allantois, enveloped by the base of the amnion, together form the *umbilical cord.* At birth, the fœtal membranes are shed, the intra-abdominal portion of the allantois persisting as a cord, the *urachus.*

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[1] The histological structure of the placenta and the various modifications seen in the maternal mucous membrane cannot be described here; it is, however, important to remember that there is no direct communication between the maternal and fœtal blood, and that the maternal capillaries usually enlarge to form sinuses, the walls of which become invaginated by the villi; thus the latter are covered by an epithelium furnished by the maternal tissues (Fig. 334). In some cases (*e.g.* Mole) part of the maternal tissue is absorbed in the uterus.

I. **URINOGENITAL ORGANS.**

a. GENERAL PART.

The first traces of the urinary and generative organs of Vertebrates arise from the mesoderm, and are closely connected with one another genetically as well as morphologically and physiologically.

I. URINARY ORGANS.

As a rule, the development of the urinary organs from their first rudiments to their final form extends through a relatively long period, and the higher the animal in question, the longer this period is. Unlike other organs, they do not reach their permanent form step by step, without a break, but consist of a series of organs, each of which has a similar function (viz., that of filtration and excretion) and corresponds to a definite ontogenetic stage, after which it is replaced functionally by another organ of the series, and may then in part take on physiological relations to the generative organs. In consequence of this peculiarity, these developmental stages of the excretory organs of Vertebrates can also be recognised phylogenetically, and are represented by the paired organs known respectively as the *fore-kidney* or *head-kidney* (*pronephros*), *mid-kidney* (*mesonephros*), and *hind-kidney* (*metanephros*).

The number of urinary organs constituting the series corresponds in general to the position of the animal in the vertebrate scale. Thus so far as is known at present, the excretory organs of Amphioxus and apparently of Myxinoids correspond to a single set; in all the true Fishes and in Amphibians, there is a provisional (pronephric) and a permanent (mesonephric) organ, while in the Amniota both pronephros and mesonephros are provisional and become replaced functionally by a third organ, the metanephros.

All these organs consist essentially of epithelial canals or tubules which arise from or close to that part of the mesoderm which primarily connects the segmented somites with the lateral plates (cf. p. 9) and is therefore often known as the *nephrotome*, to distinguish it from the myotome above and the lateral plates of

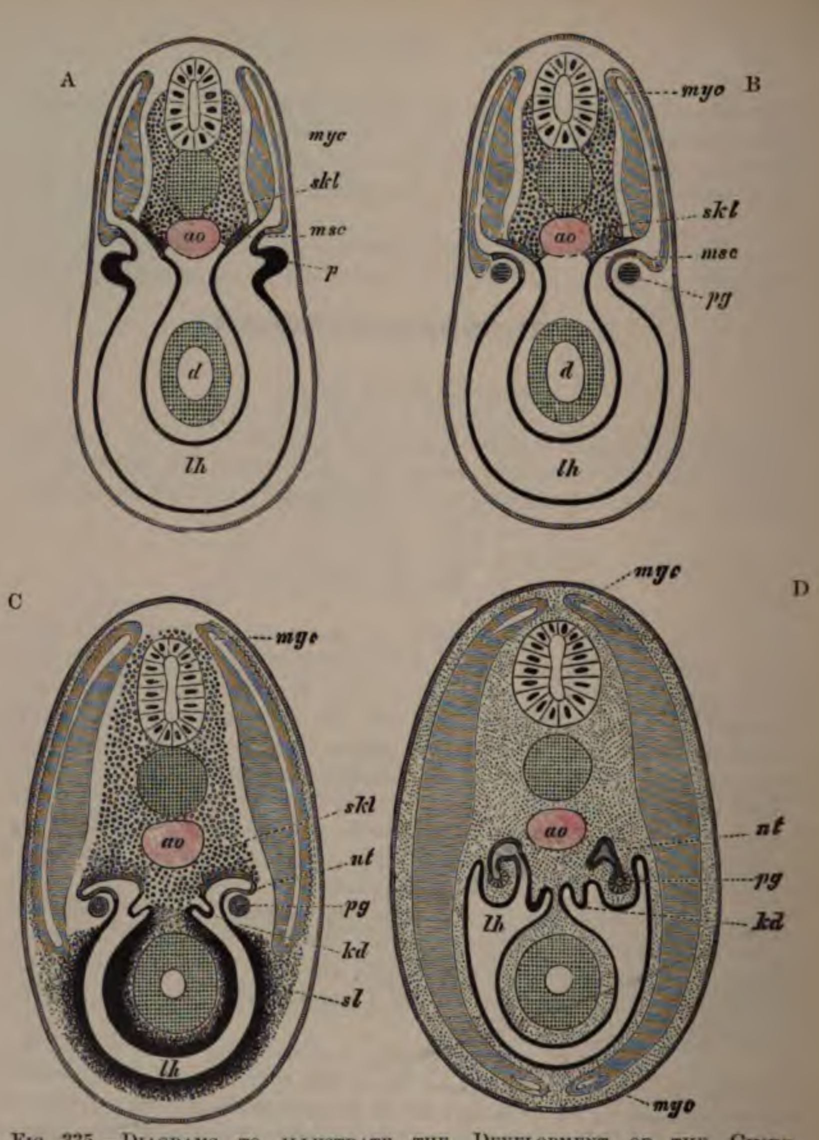

FIG. 335.—DIAGRAMS TO ILLUSTRATE THE DEVELOPMENT OF THE CHIEF PRODUCTS OF THE MESODERM. (After J. W. van Wijhe.)

A and *B*, transverse sections through an embryo in which the myotomes are beginning to become separated from the middle portions of the mesoderm, which includes the nephrotomes, *A* being in the pronephric, and *B* in the mesonephric regions. *C*, the same, shortly after this separation is completed, and *D*, later stage, in which the myotomes have extended dorsally and ventrally so as to surround the body, and have nearly lost their cavities.

ao, aorta, above which is the notochord, and above this again the medullary cord; *d*, intestine; *kd*, gonad; *lh*, general cœlome; *msc*, portion of cœlome connecting general cœlome with its portion in the myotome (myocœle, *myc*); *nt*, nephrotome or mesonephric tubule; *p*, pronephros; *pg*, pronephric or segmental duct; *skl*, sclerotome, which gives rise to the skeletogenous layer from which the vertebral column arises; *sl*, mesenchyme of the lateral plates.

mesoderm below, the cœlome primarily extending upwards through both nephrotome and myotome (cf. Fig. 335).

Pronephros.

As a rule, the rudiments of the pronephros can be recognised in the anterior segments of the trunk, and its glandular canals, extending in the transverse plane of the body, must be distinguished from the primary *pronephric* (*archinephric* or *segmental*) *duct* (Figs. 335–337), which passes backwards to open into or close behind the cloaca. Each canal communicates on the one hand with the cœlome by means of a ciliated, funnel-shaped aperture or *nephrostome*, and on the other with the pronephric duct. A projection of the inner wall of the cœlome arises right and left of the mesentery, projecting towards each canal, and into this branches from the aorta extend, each giving rise to a rete mirabile consisting of a coiled tuft of capillaries or *glomerulus*, by means of which water is filtered out from the blood: several glomeruli may unite to form a *glomus* (Fig. 337). In many Vertebrates, the parietal and visceral layers of the peritoneum in the anterior part of the cœlome unite around the glomeruli and nephrostomes so as to form cœlomic pronephric chambers or capsules more or less completely shut off from the rest of the body-cavity (Fig. 336).

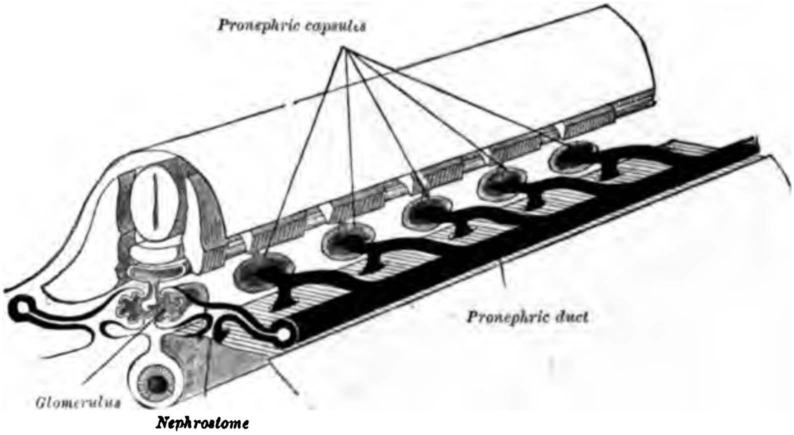

FIG. 336.—DIAGRAM OF THE PRONEPHROS SHOWING THE FORMATION OF THE GLOMERULI. (After Felix.)

A broad strip of the ectoderm and the ventro-lateral portions of the mesodermic segments are removed, and the pronephric duct and tubules are seen above the dorsal side of the cœlomic wall (transversely lined).

In Myxinoids the glandular pronephric rudiment extends along almost the whole length of the cœlome, but in other Vertebrates (*e.g.* Elasmobranchii and Amniota) it is more or less shortened and consists of only a small number of canals: this is doubtless due to a secondary reduction, which also affects the glomeruli.

The anterior part of the pronephric duct is formed by the fusion of the distal ends of the pronephric tubules: the middle and posterior parts of the duct arise in various ways in different Vertebrates, and are developed from before backwards.

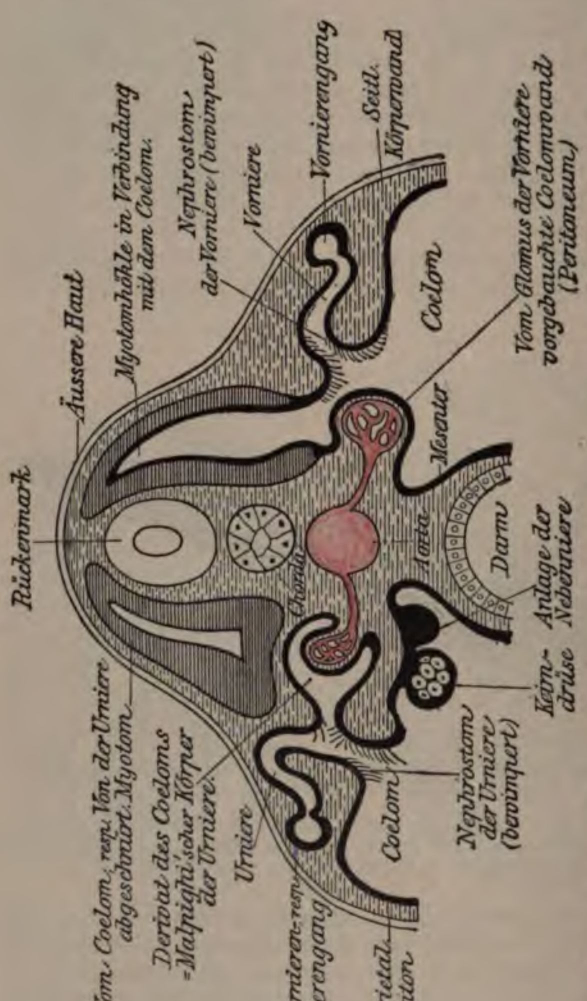
Rückenmark
Äussere Haut
Vom Coelom, resp. Von der Urniere abgeschnürt. Myotom
Myotomhöhle in Verbindung mit dem Coelom.
Derivat des Coeloms =Malpighi'scher Körper der Urniere.
Nephrostom der Vorniere (bewimpert)
Urniere
Vorniere
Chorda
Vornieren- resp. Urnierengang
Vornierengang
Parietal. Periton
Coelom
Seitl. Körperwand
Aorta
Mesenter
Coelom
Nephrostom der Urniere (bewimpert)
Darm
Vom Glomus der Vorniere vorgebauchte Coelomwand (Peritoneum)
Keimdrüse
Anlage der Nebenniere

FIG. 337.—DIAGRAMMATIC TRANSVERSE SECTION ILLUSTRATING THE PRIMARY RELATIONS OF THE PRONEPHROS (ON THE RIGHT) AND MESONEPHROS (ON THE LEFT) WITH THEIR DUCTS.

In the middle line are seen, from above downwards, the spinal cord, notochord, aorta, and intestine. On the right the cavities of the myotome and the cœlome are seen to be continuous, and a pronephric tubule (*Vorniere*), the pronephric duct (*Vorniergang*), and the glomus are shown. On the left, the cavity of the myotome has become shut off from the cœlome, and the mesonephric tubule (*Urniere*) and its duct, as well as a Malpighian capsule, are shown. Between the ciliated nephrostome of the mesonephric tubule and the intestine are seen the rudiments of the gonad (*Keimdrüse*) and adrenal (*Nebenniere*).

It is very probable that the pronephros at one time extended further back—possibly along the whole length of the trunk, and then became reduced owing to the development of another set of urinary tubules constituting the *mesonephros.*

Mesonephros.

The *mesonephros* or *Wolffian body* has usually a much greater extent than the pronephros: it is originally strictly segmental, in correspondence with the mode of development of the mesodermic somites. The tubules of which it is composed correspond with those parts of the mesoderm described above as the nephrotomes[1] (p. 441), which become separated from the somites but retain their connection with the general body-cavity, into which each of them opens by a ciliated nephrostome,[2] the other end becoming connected with the pronephric duct, which thus now serves as a mesonephric duct.

The tubules then increase in length, each becoming coiled into an S-shape and differentiated into several portions, the middle one expanding to form a vesicle (Bowman's capsule), into which a glomerulus formed on a branch of the aorta becomes invaginated, the whole constituting a Malpighian capsule (Fig. 337). It will be noticed that the glomeruli are here formed in a different manner to those of the pronephros, which arise on the wall of the general body-cavity.

The further development of the mesonephros varies greatly in different Vertebrates: in many Fishes it serves exclusively as a urinary organ, but in Plagiostomes and higher forms it also takes on relations to the generative apparatus, giving rise to the *rete* and *vasa efferentia* of the testis, as well as to part of the *epididymis* or *parorchis,* and, in Amniota, to other more or less vestigial organs of secondary importance (*parovarium, parosphoron, hydatid of Morgagni, paradidymis,* cf. Fig. 339). Nevertheless, it may still serve as the permanent urinary organ (Elasmobranchs, Amphibians), or may more or less entirely disappear as such (Amniota); in the latter case, a third series of tubules is formed, giving rise to a *metanephros,* or hind-kidney, with which is connected a *metanephric duct* or *ureter.*[3]

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[1] These, as already mentioned, are primarily hollow cœlomic canals, but in Sauropsida and Mammalia they are at first solid and become hollowed secondarily.

[2] The nephrostomes may be wanting, and this is especially the case in the higher types, owing to the early separation of the tubules from the cœlome as well as from the somites.

[3] The fact that in certain Lizards and Mammals larger or smaller portions of the mesonephros retain their urinary function for a time in post-embryonic stages, indicates that some of the ancestors of the Amniota retained the mesonephros throughout life as a functional excretory organ, before the complete differentiation of the metanephros. On the other hand, the mesonephros is so much reduced in the embryos of certain Mammals (*e.g.* Mouse) that it cannot have any importance as a urinary organ, the excretory function here being probably performed by means of the all[illegible] those of the umbilical cord.

Metanephros.

All the tubules of the mesonephros, as well as the coiled portions of the tubules and the glomeruli of the metanephros, arise essentially from the same matrix (the "nephrogenetic blastema"), the latter organ becoming later differentiated than the former: the straight, collecting portions of the metanephric tubules, on the other hand, originate as outgrowths from the mesonephric ducts, as do also the metanephric ducts (ureters), and, in Mammals, the pelvis of the kidney. The definitive kidney of the Amniota is therefore not a new organ, but corresponds to a well-developed and specialised posterior portion of the mesonephros, this specialisation having come about owing to a still further separation of that part of the kidney duct which retains its original function from that part which is taken into the service of the generative organs. Nephrostomes are wanting in the hind-kidney. The posterior end of the ureter loses its connection with the mesonephric duct and opens independently either into the cloaca or into a urinary bladder (Figs. 338, 339, and 357–364).

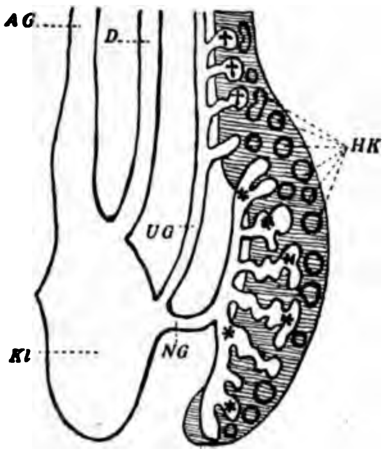

Fig. 338.—Diagram illustrating the Genetic Relations between the Mesonephros and Metanephros. (Modified from Schreiner.)

AG, allantoic duct; *D*, intestine; *HK*, urinary tubules arising in the nephrogenetic blastema; *Kl*, cloaca; *NG*, metanephric duct; **, outgrowths from metanephric duct; ††, outgrowths from mesonephric duct (*UG*).

Thus it will be seen that the distinction between the pronephros and mesonephros is much greater than that between the latter and the metanephros; all three organs, however, are derived from the same matrix, and merely represent three generations of the same ancestral organ.

The Male and Female Genital Ducts.

In certain lower Vertebrates (Elasmobranchs) a second duct, known as the *Müllerian duct*, becomes differentiated from the primary mesonephric duct, and takes on an important relation to the female generative organs, serving as an nveying the sexual products to the exterior, and ction

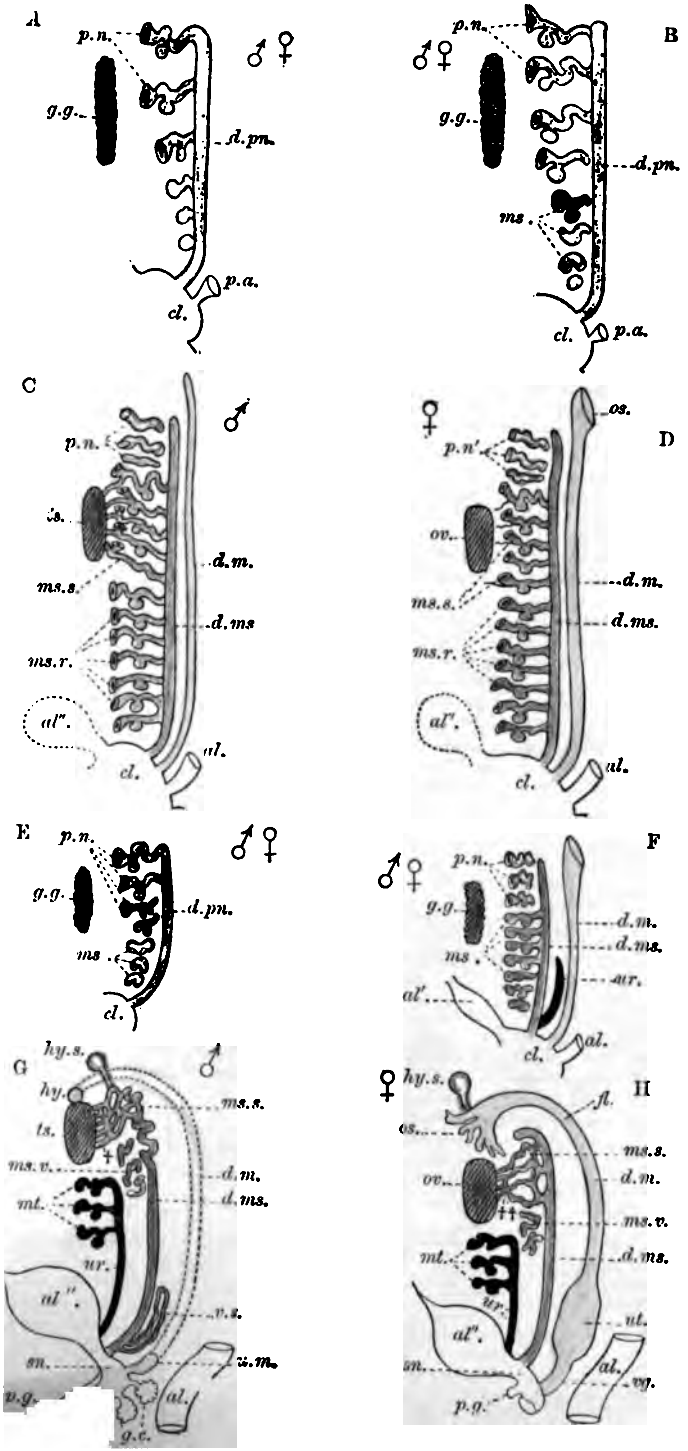

FIG. 339.—For description see next page.

FIG. 339.—A SERIES OF DIAGRAMMATIC FIGURES ILLUSTRATING THE ACCOUNT OF THE COMPARATIVE MORPHOLOGY OF THE URINOGENITAL ORGANS OF THE VERTEBRATA GIVEN IN THE FOLLOWING PAGES.

A, the pronephros stage of the Anamnia; B, a later stage of the same; C, the urinogenital apparatus of the male Amphibian; D, the same of the female; E, pronephros stage of the Amniota, the mesonephros as yet rudimentary; F, urinogenital apparatus of the Amniota at a stage at which the sexes are not differentiated; G, urinogenital apparatus of male Amniota; H, the same of female Amniota.

al, rectum; *al′*, *al″*, allantois or urinary bladder; *cl*, cloaca; *d.m*, Müllerian duct, which in Mammals becomes differentiated (Fig. H) into the Fallopian tube (*fl*), the uterus (*ut*), and the vagina (*vg*); *d.ms*, duct of the mesonephros, which in male Amphibians and Elasmobranchs becomes (Fig. C) the urinogenital, and in females (Fig. D) the urinary duct. In the male Amniota it gives rise to the seminal duct (Fig. G), and in the female to Gärtner's duct (Fig. H); *d.pn.*, duct of the pronephros; *g.c*, Cowper's glands; *g.g*, gonads, undifferentiated stage; *hy*, and *u.m* (Fig. G), unstalked hydatids and uterus masculinus (vestiges, in the male, of the Müllerian duct, *d.m*); *hy.s*, stalked hydatid; *ms*, the developing mesonephros; *ms.r*, renal portion of mesonephros; *ms.s*, part of the mesonephros becoming converted into the epididymis and parovarium; *ms.v*, vestiges of the mesonephros (paradidymis and paroophoron); *m.t*, the definitive kidney or metanephros of the Amniota; *os*, abdominal aperture of oviduct; *ov*, ovary; *p.a*, abdominal pore; *p.g*, penis, clitoris; *p.n*, pronephros; *su*, urinogenital sinus; *ts*, testis; *ur*, ureter; *v.s*, seminal vesicle, an outgrowth of the duct of the mesonephros; †, rete and vasa efferentia testis; ††, a network homologous with these structures at the hilum of the ovary.

TABULATED RÉSUMÉ OF THE FACTS PICTORIALLY ILLUSTRATED ON PAGE 447.

	Anamnia.	Amniota.
Pronephros. Male and Female.	Develops in all Anamnia, but rarely persists as a permanent excretory organ.	Still develops in the Amniota, but as an excretory organ undergoes entire degeneration in the embryo.
Duct of Pronephros. Male and Female.	In Elasmobranchs and some Amphibians appears to give origin by subdivision to the mesonephric (Wolffian) and Müllerian ducts. In other Amphibia, becomes converted into the mesonephric duct. Its fate in other Anamnia is not yet fully investigated.	Persists as the mesonephric (Wolffian) duct, and contributes to some extent in the formation of the Müllerian duct.
Mesonephros. Male and Female.	Serves in all Anamnia as a urinary gland. In Plagiostomes, Ganoids, Dipnoans, and Amphibians, a certain portion becomes related to the male genital apparatus, the remaining portion persisting as a permanent kidney.	Loses its renal function in all Amniota (as a rule in the embryo), and becomes vestigial, except so far as it becomes an accessory portion of the genital apparatus in the male.

TABULATED RÉSUMÉ—(*Continued*).

		Anamnia.	Amniota.
Mesonephros.	Male.	A portion (except in Cyclostomes, Teleosts and (?) Holocephali) becomes related to the testis and functional in the transmission of the sperms, the distal retaining its renal function.	The anterior end becomes the rete and vasa efferentia testis, the caput epididymis, and perhaps also the stalked hydatid of Morgagni: the posterior end becomes the paradidymis (Giraldé's organ).
	Female.	Persists as the kidney.	The greater part of the anterior portion becomes the parovarium, the posterior the paroophoron.
Duct of Mesonephros.	Male.	Serves in Teleosts merely as a urinary duct. In Elasmobranchs, Ganoids, Dipnoans, and Amphibians serves as the urinogenital duct.	The anterior portion becomes the corpus and cauda epididymis and the posterior the spermiduct (vas deferens).
	Female.	Serves exclusively as the duct of the mesonephros, *i.e.*, the urinary duct.	The greater part, as a rule, degenerates; the anterior portion may be retained in a vestigial form in the region of the parovarium. In certain cases it may persist, as a whole, as Gärtner's canal. The posterior end becomes the organ of Weber.
Müllerian Duct.	Male.	In Elasmobranchs it degenerates in post-embryonic life, but vestiges of its anterior portion are retained. Its existence in most other Fishes is doubtful. In Dipnoans and Amphibians it is retained, at any rate for some time, for its whole length, in a functionless and often but little degenerate condition.	The anterior portion becomes the unstalked hydatid of Morgagni, the posterior, in some Mammals, the so-called "uterus masculinus" (prostatic vesicle). In exceptional cases the whole is retained as Rathke's duct. In Sauropsida the posterior part usually disappears.
	Female.	When present, gives rise to the whole genital duct.	Gives rise to the whole genital duct.
Metanephros and Ureter.	**Male and Female.**	Probably unrepresented.	**Arises in part (ureter and collecting ducts) from the posterior end of the mesonephric duct, and in part (secreting elements) as a caudal extension of the mesonephros.**

with the cœlome anteriorly by means of an aperture derived from the anterior nephrostomes; only vestiges of this duct are retained in the male (Fig. 339). Its formation is probably due to a division of physiological labour, the primary mesonephric duct having originally served to carry to the exterior the generative cells of both sexes as well as the secretion of the primary urinary tubules, through the nephrostomes.

The remaining part of the mesonephric duct (*Wolffian duct*) still serves as a urinogenital duct in male Elasmobranchs and Amphibians. In the Amniota, in which the mesonephros gives up its function as a urinary organ, the Wolffian duct serves exclusively as a spermiduct (*vas deferens*).[1] Its coiled anterior portion takes part in the formation of the epididermis.

The Gonads ("Generative Glands").

The sexual cells, which give rise to the *ova* and *spermatozoa*, originate from the germinal epithelium, which corresponds to a differentiation of part of the cœlomic or peritoneal epithelium on the dorsal side of the body-cavity on either side of the mesentery, and into which the adjacent mesodermic stroma penetrates; thus a pair of **gonads** or "sexual glands" is formed (Fig. 337). Primitively the gonads had a segmental arrangement, and extended throughout a greater number of body-segments.

The primitive germinal cells are at first all similar to one another, but in the course of development a differentiation takes place, resulting in the formation of a male or a female gonad, *i.e.*, a **spermary** (**testis**) or an **ovary**.

The mode of development of the ova and spermatozoa is briefly as follows:—

Ova.—The cells of the germinal epithelium grow inwards amongst the connective tissue stroma of the ovary, or into its cavity when hollow, in the form of clustered masses which may become separated off from the periphery: certain of these cells increase in size more than the others, and give rise to the *ova*, while the smaller cells form an investment of *follicle* round them, and may serve as nutritive material. The investing cells multiply, and in Mammals a cavity containing a fluid is formed in the middle of each follicle (Fig. 340): the main mass of the follicular cells which enclose the ovum project, as the *discus proligerus*, into the cavity of the follicle. When ripe, the ovum, surrounded by a vitelline membrane, comes to the surface of the ovary and breaks through into the abdominal cavity;[1] it then passes into the cœlomic aperture of the oviduct.

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[1] The mode of development of the Müllerian duct in the Amphibia, Sauropsida, and Mammalia has undergone secondary modifications, the details being to some extent still under controversy; but at any rate it appears to be certain that in the Amniota its anterior end arises from a groove in the cœlomic epithelium, while its posterior part, closely connected with the mesonephric duct, is formed by a gradual backward growth of an originally solid epithelial cord. This later loses its connection with the cœlomic epithelium, develops a lumen, and breaks through into the cloaca.

Spermatozoa.—In the male, as in the case of the female, primitive germinal cells can be at first distinguished in the development of the generative elements. These give rise to a series of *seminal tubules* (Fig. 363), containing larger and smaller cells; the former undergo division to form the active and relative minute *sperms* or *spermatozoa*. The nucleus gives rise to the so-called "head" of the sperm, while the surrounding protoplasm becomes differentiated to form the motile "tail," the "neck" arising from the centrosome of the cell (p. 3).

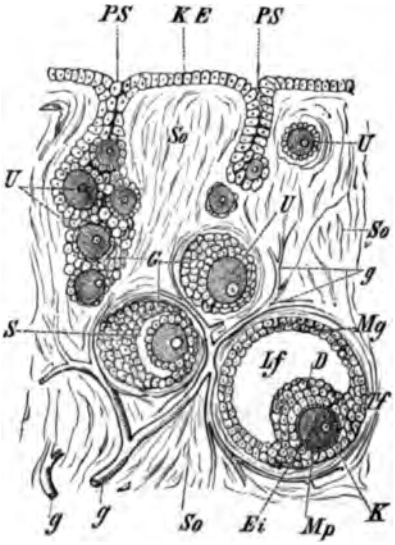

Fig. 340.—Section through a Portion of the Ovary of a Mammal, showing the Mode of Development of the Graafian Follicles.

D, discus proligerus; *Ei*, ripe ovum, with its germinal vesicle (*K*) and germinal spot; *KE*, germinal epithelium, ingrowths from which extend into the stroma of the ovary to form the ovarian tubes (*PS*): the stroma is penetrated by vessels (*g*, *g*); *Lf*, liquor folliculi; *Mp*, zona pellucida, showing radiated structure; *S*, cavity between the follicular epithelium (tunica granulosa, *Mg*) and the primitive ova; *Tf*, theca folliculi; *U*, *U*, primitive ova.

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[1] In Mammals a certain amount of blood is poured out through the broken ends of the vessels in the stroma of the ovary into the cavity of the follicle vacated by the ovum; around it a cellular investment is formed from the follicle-cells, and further modifications take place, resulting in a body of yellow colour, known as the *corpus luteum*, the function of which may possibly be that of a "gland with internal secretion" (cf. under Pancreas, Adrenals, &c).

b. SPECIAL PART.

URINARY ORGANS.

In **Amphioxus** a series (90 or more) of independent segmental tubules are present on either side in the reduced section of the cœlome situated on the dorsal side of the pharynx, in close relation to the branchial blood-vessels.

Each tubule is partly glandular and partly ciliated, and gives off several knobs provided with peculiar club-shaped cells projecting into the cœlome and corresponding to closed nephrostomes: its other end opens into the atrial or peribranchial chamber (p. 352) by a single aperture.[1] The segmental arrangement of the tubules in the adult corresponds to that of the branchial apparatus, and not to that of the myotomes. No tubules are present posteriorly to the pharynx.

Cyclostomes.—In the Petromyzontidæ, the excretory system resembles that of the Amphibia much more closely than in the Myxinoidei. In the former, rudiments of at least thirteen pronephric tubules gradually appear, but only the five most anterior of these become functional. In Ammocœte larvæ about 10 cm. in length, the pronephros reaches its highest stage of development, and by this stage a mesonephros has also arisen from the cœlomic epithelium, so that for some time both organs are functional (Fig. 341). As the mesonephros slowly develops further, from before backwards, the pronephros becomes gradually reduced, and eventually also a reduction takes place of about two-fifths of the entire mesonephros also.

Observations on the excretory organs of Myxinoids are still incomplete, and it is uncertain whether both pronephros and mesonephros are developed, or whether only one pair of these organs is represented.

In none of the Cyclostomes does the kidney come into relation with the generative organs, and its duct, which opens into the urinogenital sinus, probably in all cases represents the unaltered pronephric duct.

Elasmobranchs.—In these Fishes, the transitory pronephros has a rudimentary character, and is very variable: it usually only extends over 3–5 body-segments (Raia, Torpedo)—more rarely over 7–8 segments of the embryo, and apparently has no excretory function. As already mentioned (p. 446) a differentiation of the primary mesonephric duct into Wolffian (secondary mesonephric)

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[1] It is very doubtful whether the suggestion is justified that these epibranchial tubules correspond to some extent to the pronephros of the Craniata, and the peribranchial chamber to its duct.

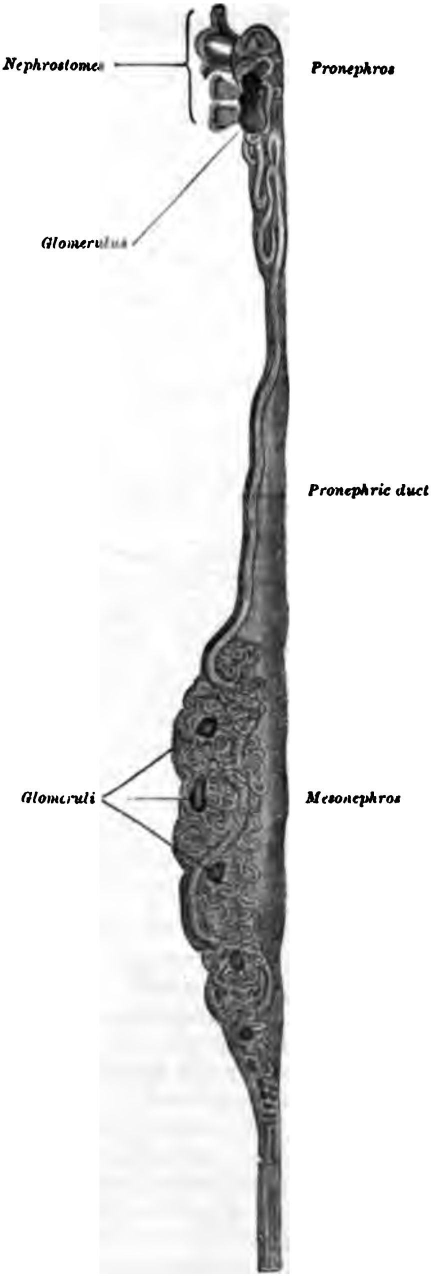

FIG. 341.—THE EXCRETORY SYSTEM OF A *Petromyzon fluviatilis*, 22 MM. IN LENGTH, from the inner side. (After Wheeler.) About half the entire length of the primary urinary duct is represented, and behind the pronephros it is greatly coiled. Four pronephric nephrostomes and a folded glomerulus are present, and between the pronephros and mesonephros is a portion wanting in tubules.

and Müllerian ducts, takes place, and a distinction between an anterior, a middle, and a posterior section of the mesonephros may be observed in Plagiostomes (Figs. 339, 349). In the male the anterior portion (*epididymis* or *parorchis*) comes into connection with the testis by means of small ducts, the *vasa efferentia*, and in the female undergoes reduction: the middle portion usually becomes considerably reduced, especially in the female, but its ducts still communicate with the Wolffian duct, which is more or less dilated at its posterior end and in the male serves mainly as a vas deferens: the large posterior portion forms the essential part of the kidney, and empties its secretion by means of special urinary ducts, some of which unite with one another, into the urinogenital sinus.

This differentiation of the hinder part of the mesonephros, and the formation of special ducts in connection with it, seems, in a sense, to foreshadow the condition which occurs in the Amniota (p. 446).

In the Holocephali no sexual portion of the kidney can be distinguished, and the anterior part in the male Callorhynchus is much larger and more massive than the posterior section, which, as in Plagiostomes, is provided with special ducts.

The kidney is very variable in form and size: its outer border is usually notched, and this, together with the arrangement of the nephrostomes in the embryo, points to the original segmental arrangement of the organ. The segmental character, however, disappears later on; in the adult the nephrostomes are much less numerous than the vertebræ of this region, but their number and size vary much in different genera and even in individuals, and they do not persist in all (*e.g.* Carcharias, Mustelus, Echinorhynchus, Myliobates, Raia).

Teleostomes.—The larval pronephros of Ganoids consists of a varied number of canals, the segmental arrangement of which has so far not been accurately ascertained.[1] In the definitive kidney (mesonephros) a segmental arrangement is recognisable. In Sturgeons, its connection with the cœlome by means of nephrostomes takes place only after the individual canals have become connected with the pronephric duct.

The pronephros in the majority of Teleosts has only a temporary significance, and extends over from one to five segments.[2] The mesonephros constitutes the excretory organ of the adult, and consists of a narrow band varying in size and diameter in different regions, situated on the dorsal side of the body-cavity, between the vertebral column and the swim-bladder. Secondary fusions between the two kidneys often occur.

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[1] The nephrostomes of the pronephros open either directly into the cœlome or into a space shut off from the latter which encloses the more or less folded glomus (p. 443).

[2] It persists in Lepidogaster, Fierasfer, a

The urinary duct in both groups probably represents the pronephric duct, and may lie more or less freely, or be embedded in the substance of the kidney. Posteriorly the two ducts usually fuse together and become expanded to form a kind of urinary bladder, as is also the case in Ganoids (cf. Figs. 350 and 351); in its formation, however, the ectoderm of the cloaca also takes part. The bladder usually opens behind the anus—either independently, or together with the genital ducts—by a simple pore, or on the summit of a urinogenital papilla. Thus a differentiation of the pronephric duct into a Wolffian and a Müllerian duct is not known to occur in Teleostei, nor does the mesonephros come into connection with the gonads: the early development both of the pronephros and mesonephros exhibits special peculiarities.

A close examination of the organ, which appears to the naked eye as the kidney in Teleosts and Ganoids, shows that a larger or smaller portion of it—more particularly the anterior part—consists of an adenoid or lymphoid tissue, comparable to the hæmolymph glands described on p. 435.

Dipnoans.—The pronephros of the larva consists of several tubules, and possesses two nephrostomes. The mesonephric tubules have at first a strictly segmental arrangement, but later are more numerous than the corresponding myotomes: they possess no nephrostomes. The mesonephros forms the definitive kidney; it is relatively longer in Protopterus than in Ceratodus, extending through a considerable portion of the body-cavity, being narrow anteriorly, and gradually broadening out further back (Fig. 352). In Lepidosiren and Protopterus the posterior instead of the anterior end of the kidney comes into relation with the testis and so may be spoken of as a "posterior epididymis." In Protopterus this is fused with its fellow and covered with black pigment. The kidneys are invested by lymphoid and adipose tissue, especially on their lateral and posterior borders. In the female, the mesonephric ducts communicate with the cloaca independently, behind the genital papilla: in the male they open dorsally into the base of the cloacal cæcum (Fig. 247) on a single (Protopterus) or paired (Lepidosiren) papilla. The cloacal cæcum is possibly comparable to the sperm-sac of Elasmobranchs, and to the urinary bladder of Teleostomes.

Amphibians.—Although the primary pronephric rudiments extend over a large number of segments, the number of actual pronephric canals is usually limited to 12 or 13 in the Gymnophiona, three in the Anura, and two in the Urodela.[1]

Thus the most typical condition of the pronephros amongst Vertebrates is met with in the embryos of Gymnophiona, and this primitive condition is also seen in the mesonephros, which consists of long, narrow, varicose bands, usually extending from the heart to the anterior part of the cloaca, which latter is often much

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[1] The pronephros undergoes degeneration at the beginning of metamorphosis in Urodeles and Anurans, and at a relatively earlier stage in the Gymnophiona.

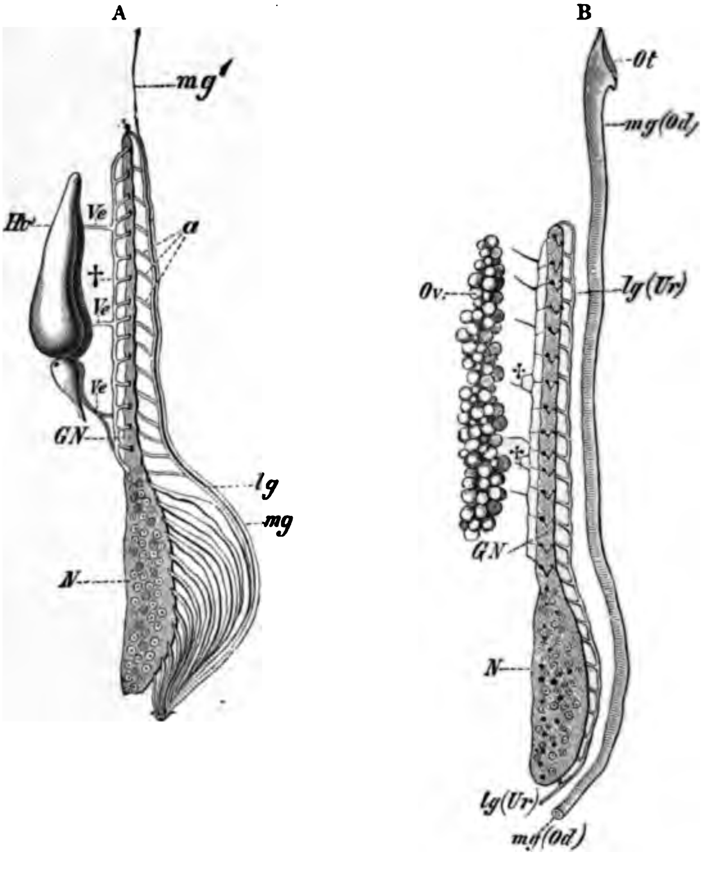

FIG. 342.—DIAGRAM OF THE URINOGENITAL SYSTEM OF (A) A MALE AND (B) A FEMALE URODELE; FOUNDED ON A PREPARATION OF *Triton tæniatus.* (After J. W. Spengel.)

a, collecting tubes of the mesonephros, which open into the Wolffian (urinogenital) duct (*lg*); in the female the latter serves simply as the urinary duct (*Ur*), and the system of the vasa efferentia (testicular network) is vestigial; *GN*, anterior portion of kidney (epididymis of the male); *Ho*, testis; *mg*, *mg*¹, Müllerian duct; *N*, posterior non-sexual portion of kidney; *Ot*, cœlomic aperture of Müllerian duct (oviduct, *Od*); *Ov*, ovary; *Ve*, vasa efferentia of testis which open into the longitudinal canal of the mesonephros, †.

elongated. In the embryo they consist of definite masses which are arranged metamerically, and in each of them a nephrostome, and an excretory duct can be disti

354). This condition sometimes persists in the anterior portion of the kidney, but owing to secondary processes of growth, as many as twenty nephrostomes are later on met with in a single body-segment. The number of nephrostomes in the entire kidney may amount to a thousand or more. As regards the urinary duct and the relations of the entire renal apparatus to the generative organs, the Gymnophiona in all essential points resemble other Amphibia.

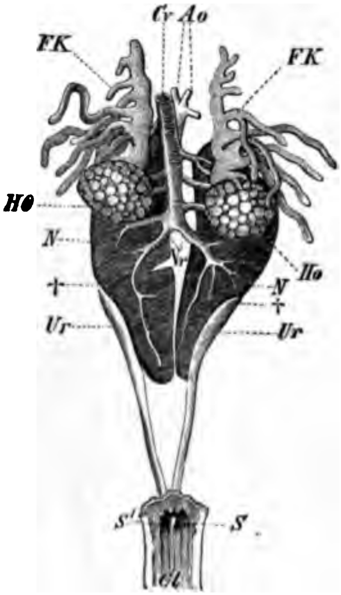

Fig. 343.—Male Urinogenital Organs of *Rana esculenta*. From the ventral side.

Ao, aorta; *Cr*, postcaval vein; *FK*, corpus adiposum; *Ho*, testis; *S*, *S'*, apertures into the cloaca (*Cl*) of *Ur*, urinogenital (Wolffian) ducts, which appear on the lateral surface of the kidneys at †; *Vr*, revehent renal veins.

The kidneys of Urodela and Anura are situated in the usual position on the dorsal side of the body-cavity; in the former they are band-like and more extended longitudinally than in the latter, in which they are shorter and more compact, and are confined to the middle portion of the cœlome.

In Urodeles they always consist of a narrow anterior, and a broader and more compact posterior portion. The latter, as in Elasmobranchs, gives rise to the functional kidney, while the former becomes connected in the male with the generative organs. Delicate vasa efferentia, developed from the mesonephros, in all cases pass out from the testis (Figs. 342, 355) into the substance of the kidney, and there open into the mesonephric tubules; they may either enter the kidney direct, or else open first into a longitudinal collecting duct, from which fine canals pass to the tubules. Thus the seminal fluid passes through the nephridia as well as through the Wolffian duct, which serves as a urinogenital duct.

In Urodela and Anura of both sexes the Wolffian duct nearly always opens separately on either side into the cloaca, receiving first, in Urodeles, a number of ducts from the posterior part of the kidney (cf. Elasmobranchs). In Anura the Wolffian ducts pass some distance independently along the body-cavity in correspondence with the position of the kidneys, and a seminal vesicle (not present, *e.g.*, in Rana esculenta) may open into each (Fig. 344).

The ***urinary bladder***, representing the entire allantois (cf. p. 437) opens into the cloaca ventrally, opposite to the urinogenital apertures. In its simplest form it is finger-shaped (*e.g.* Siren,

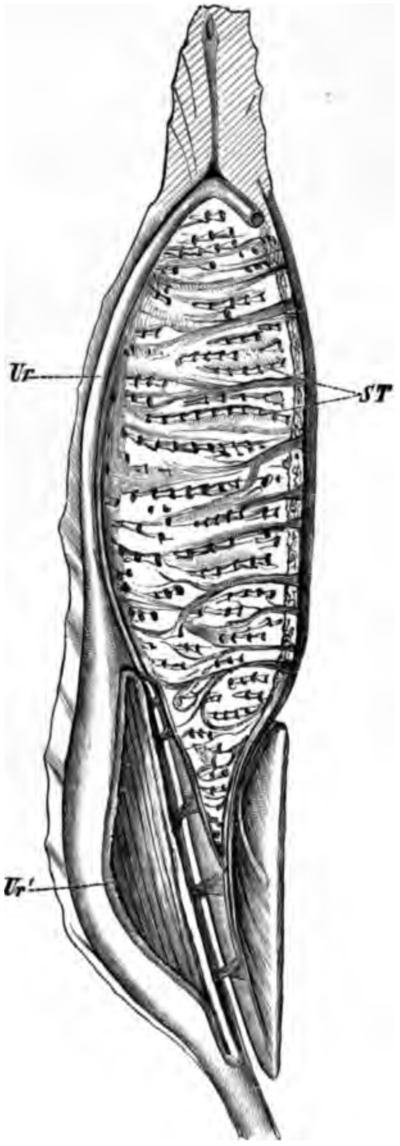

FIG. 344.—KIDNEY OF *Discoglossus pictus.* From the ventral surface, showing the nephrostomes (*St*). (After J. W. Spengel.)

Ur, urinogenital duct, enlarging at *Ur*[1] to form a seminal vesicle.

Proteus),[1] but it usually becomes swollen distally and is ofte bilobed : in Alytes and Bombinator it forms a double sac.

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[1] In Amphiuma, it is relatively very long. In the Gymnophiona, the bl *presents* certain peculiar secondary modifications.

Slight indications of a segmental arrangement are found only in the anterior sexual portion of the kidney of Urodeles; in the posterior part, and in the entire kidney of Anura, all traces of segmentation have disappeared. In both cases, however, the nephrostomes remain throughout life in great numbers on the ventral surface of the kidney, which is covered over by the peritoneum (Fig. 344). The nephrostomes are connected with the urinary tubules in larval Anura, but later on they become separated from them, and open into the efferent renal veins. In consequence of this, the body-cavity of adult Anura is a closed lymph-sinus, as in the Amniota; the peritoneal fluid, which in the larva was carried to the exterior and lost, is in the adult poured into the general circulation, like the rest of the lymph.

Reptiles and Birds.—In the Sauropsida, as in the Mammalia, the mesonephros, so far as it is retained in the adult, is usually entirely distinct from the functional excretory apparatus; this consists of a metanephros, entirely wanting in nephrostomes (cf. p. 446).

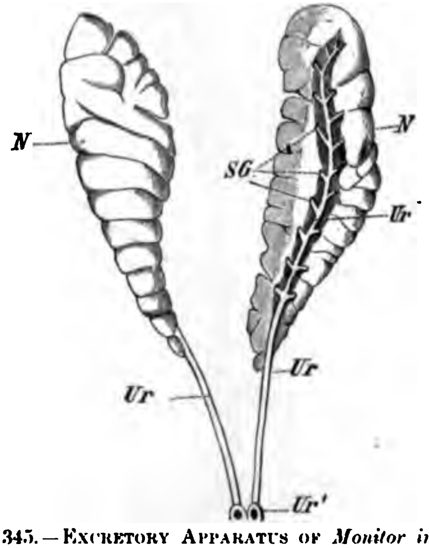

FIG. 345.—EXCRETORY APPARATUS OF *Monitor indicus*.

The right kidney is shown in its natural position, while the left is turned on its longitudinal axis, so that the ureter and collecting tubes are visible. The urinary bladder is not represented.

N, *N*, kidneys; *SG*, collecting tubes which open into the ureter (*Ur*, Ur^2); Ur^1, aperture of ureter into the cloaca.

The metanephros never extends so far along the body-cavity as does the mesonephros; as a rule it has the form of a small, compact or lobulated organ, usually situated in the posterior half of the b[illegible]vity, or even entirely confined to the pelvic region: it has the latter position, for instance, in most Reptiles (Figs. 345, 357, 358) and all Birds (Fig. 346). The posterior end of the kidney, which is generally narrower than the rest, may even extend under the root of the tail, as in Lacerta, in which region the two organs are fused.

Thus according to the position of the kidneys, the ureters (metanephric ducts) either do not extend freely along the body-cavity, or they may have a longer or shorter free course. The latter is the case, for instance, in Crocodiles, and more especially in Birds (Fig. 346): in the latter the kidneys are closely embedded within the pelvis, and their ventral flattened surface is usually divided into lobes and is often

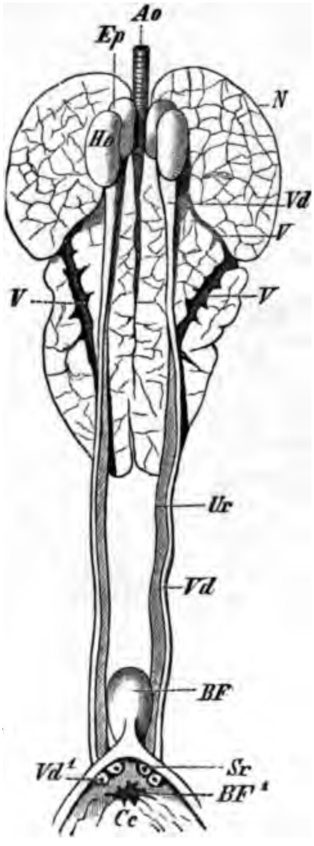

FIG. 346.—MALE URINOGENITAL APPARATUS OF HERON (*Ardea cinerea*).

Ao, aorta; *BF*, bursa Fabricii, which opens into the cloaca at BF^1; *Ep*, epididymis; *Ho*, testis; *N*, kidney; *Ur*, ureter, opening into the cloaca (*Cc*) at *Sr*; *V*, *V*, furrows on the ventral surface of the kidney in which veins lie embedded; *Vd*, vas deferens, which opens at Vd^1 on a papilla in the cloaca.

penetrated by deep furrows and clefts into which the veins extend; posteriorly they may fuse together in the middle line, as in Lizards.

There is not always a perfect symmetry between the organ of either side, and this is most marked in Snakes, in which the greatly lobulated kidneys, like those of limbless Lizards, are elongated, narrow, and band-like, in correspondence with the form of the body.

A *urinary bladder*, arising from the ventral wall of the cloaca, is present in most Lizards and Chelonians; it is more or less bilobed. A bladder is wanting in Snakes, Crocodiles, and Birds, as well as in Monitors and Amphisbænians amongst Lizards. It is derived in part from the stalk of the allantois and in part from the cloaca[1] (cf. p. 440).

Mammals.—The definitive kidneys of Mammals[2] are proportionately small, and lie on the quadratus lumborum muscle and ribs. They usually possess a convex outer, and a concave inner border; the latter is called the *hilum*, and at this point the ureters arise and the blood-vessels enter. The expanded proximal portion of the ureter is divided up to form one or more *calyces* into which small papilliform processes of the *pyramids* project (Fig. 347); on the summits of these the urinary tubules open in varying number. The calyces are continuous with a large cavity in the widened portion of the ureter called the *pelvis*, and from this the ureter (metanephric duct) passes freely backwards for some distance to open into the bladder on its dorsal side, sometimes nearer the apex, sometimes towards the fundus. The bladder communicates with the *urinogenital canal* or *urethra* (cf. under Genital organs).

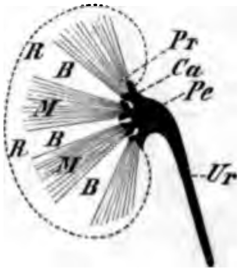

FIG. 347.—DIAGRAMMATIC LONGITUDINAL SECTION THROUGH THE KIDNEY OF A MAMMAL.

Ca, calyces; *M*, *M*, medullary substance arranged in pyramids (*Pr*); between the latter the cortical substance extends in the form of the columns of Bertini (*B*, *B*); *R*, *R*, cortical substance; *Pe*, pelvis; *Ur*, ureter.

The kidney is greatly lobulated in the embryo; this condition may remain throughout life (*e.g.* in Cetacea, Pinnipedia, Proboscidea, and certain Ungulates, Carnivores, and Primates, cf. Fig. 348), or the lobes may become more or less completely united. In the latter case the original division into lobes may still be recognised to a greater or less extent internally. A section of the kidney shows an inner layer, the *medullary substance*, arranged in the form of wedges—the urinary pyramids,—and an outer layer, or *cortical substance*, extending as the columns of Bertini between the pyramids (Fig. 347).

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[1] The urinary bladder is said to be represented in embryo Birds by an enlargement of the stalk of the allantois, and in Crocodiles by a ventral outgrowth from the cloaca.

[2] In the embryonic mesonephros, nephrostomes occur only in Echidna.

The Malpighian capsules as well as the coiled portions of the tubules, surrounded by a network of blood-capillaries, lie in the cortical substance, while the straight portions of the tubules extend through the pyramids, where they gradually anastomose to form larger collecting tubes.

The *urinary bladder* in Monotremes and nearly all Marsupials represents the whole allantois, and the ureters open at its junction with the urinogenital canal (Fig. 359). In placental Mammals, on the other hand, the greater part of the bladder is a new formation, which arises by a special differentiation of the cloaca, the latter becoming divided into a dorsal and a ventral portion by the formation of a septum. The former is continuous with the rectum, and the latter gives rise to the urinogenital canal and bladder, which is continuous distally with the stalk of the allantois from which the urachus (p. 440) and the median ligament of the bladder are formed. These two sections of the cloaca gradually become further separated from one another by the development of the *perinæum*, or space between the urinogenital

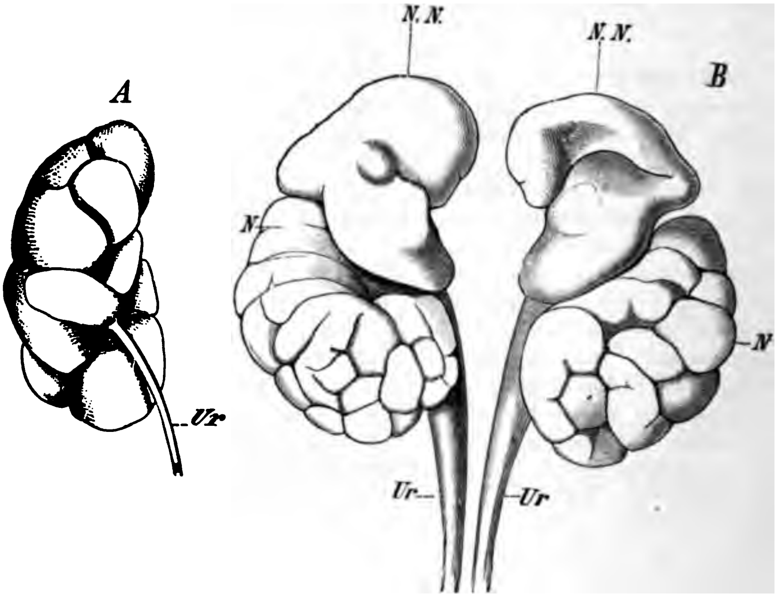

Fig. 348.—A, Right Kidney of a Deer; B, Kidneys (*N*) and Adrenal Bodies (*N.N*) of the Human Embryo. Both from the ventral side.

Ur, ureters.

and anal apertures. The bladder of the Eutheria is thus mainly, though not entirely, of endodermal origin, and the base of the allantoic stalk into which the ureters open becomes included in it.

GENITAL ORGANS.

In **Amphioxus** the gonads are developed in a part of the reduced cœlome situated on either side of the pharynx and intestine between the outer body-wall and the atrial cavity. They have a marked segmental arrangement, and each portion sheds its products independently into the atrial cavity, whence they pass out through the atrial pore (cf. p. 352 and Fig. 258). The sexes are separate, and are easily distinguishable from one another when the sexual products are ripe, although the gonads have a similar form in both sexes. The gonads, which are said to act also as excretory organs, are surrounded by blood-spaces which communicate with the portal system (Fig. 324).

In **Cyclostomes** also, generative ducts are wanting; the spermatozoa or ova are shed directly into the body-cavity, and pass through the genital pores (p. 389) into the urinogenital sinus, which in Lampreys is produced into a papilla on the apex of which the urinogenital aperture is situated. The gonad is a long, usually unpaired organ suspended, as in other Vertebrates, to the dorsal wall of the body-cavity by a fold of peritoneum, the mesoarium or mesorchium.[1]

Myxine is hermaphrodite, and the adult is either predominantly male or female. The posterior part of the gonad represents a testis, and the remainder an ovary, and either the one or the other becomes mature in each individual.[2]

In the true Fishes the gonads are only exceptionally unpaired, and even then this is only a secondary condition, due to the fusion of the two organs or to the reduction of that of one side: as in all other Vertebrates, they are originally paired. There is sometimes a want of symmetry observable between the organ of the right and left side respectively.

In the greater number of **Elasmobranchs** the ovaries are paired: but in some cases (*e.g.* Scyllium, certain Rays) only that of one side becomes developed. The oviducts, as already mentioned (p. 452) correspond to Müllerian ducts. Their anterior portion has a common opening into the body-cavity, and further back each is provided with an *oviducal* or *shell-gland*. The anterior part of the oviduct is always narrower and more delicate than the posterior, which dilates to form a kind of *uterus* in which, in viviparous forms, the embryo undergoes development. Posteriorly, the oviducts open into the cloaca somewhat behind the aperture of

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[1] In Myxinoids the genital ridge is occasionally paired.

[2] Sterile forms are also said to occur.

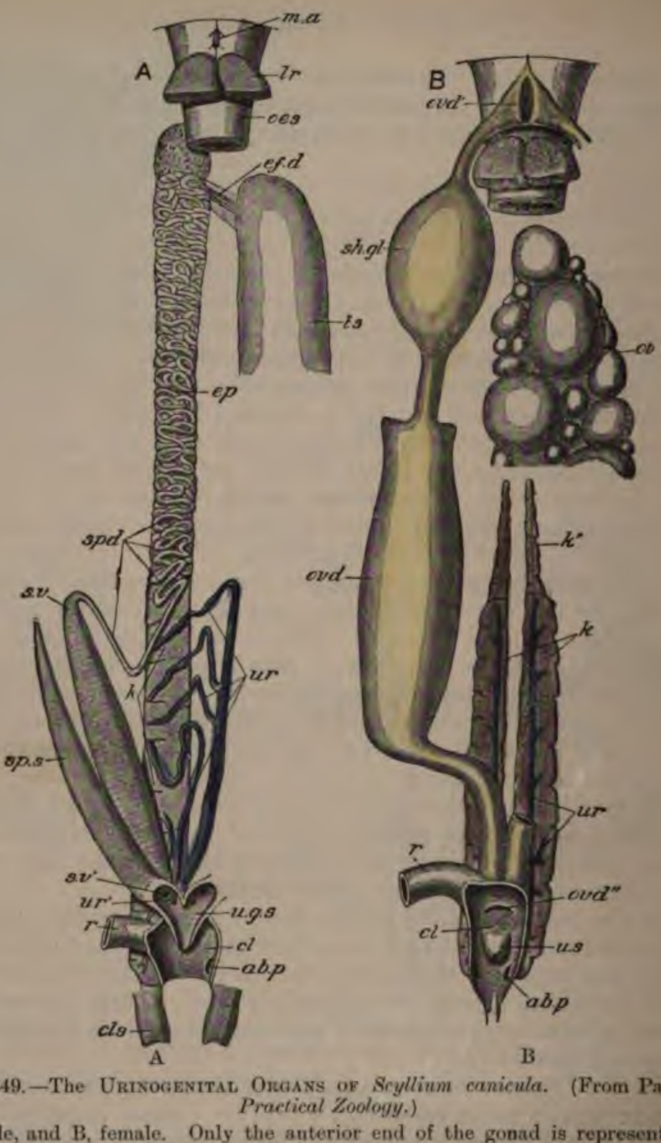

FIG. 349.—The URINOGENITAL ORGANS OF *Scyllium canicula.* (From Parker's *Practical Zoology.*)

A, male, and B, female. Only the anterior end of the gonad is represented in each figure, and except that in B both kidneys are shown, the organs of the right side only are drawn. In A the seminal vesicle and sperm-sac are dissected away from the kidneys and displaced outwards, and the urinary ducts inwards.

ab.p, depression into which the abdominal pore opens; *cl*, cloaca; *cls*, clasper; *ef.d*, vasa efferentia extending between the testis and the anterior section of the mesonephros; *e.p*, *k'*, middle section of mesonephros; *k*, posterior section of mesonephros; *lr*, anterior portion of liver; *m.d*, vestigial Mullerian duct in the male; *oes*, gullet; *ov*, ovary; *ovd*, oviduct (Müllerian duct); *ovd'* common cœlomic and *ovd''*, cloacal aperture of oviducts; *r*, rectum; *sh.gl*, shell-gland; *spd*, Wolffian duct (vas deferens); *sp.s*, sperm-sac; *s.v*, vesicula seminalis, and *s.v'*, its aperture into the urinogenital sinus; *ts*, testis; *u.g.s*, urinogenital sinus; *ur*, ducts of posterior section of kidney, and *ur'* their apertures into the cloaca; *u.s*, urinary sinus of female.

the ureters—either separately, or by a common aperture (Fig. 349). Internal fertilisation takes place by means of the claspers of the male [1] (p. 486).

In Mustelus antarcticus the uterus becomes divided into several compartments, each containing an embryo surrounded by a membrane apparently representing the horny egg-shell of other forms; in others (*e.g.* Acanthias vulgaris, Trygon pastinaca, Trygorhina fasciata, Rhinobates vincentianus), a common horny investment encloses several eggs or embryos.

The testis of Elasmobranchs is paired and symmetrical: it is oval in Chimæroids and more elongated and relatively larger in Plagiostomes, in which the two organs may become partially fused. As already mentioned (p. 454), vasa efferentia, opening into a longitudinal canal, connect each testis with the anterior end of the corresponding mesonephros (epididymis) in Plagiostomes, the coiled Wolffian duct serving mainly as a vas deferens and giving rise to a dilated portion (*vesicula seminalis*), which communicates with the urinogenital sinus; a more or less elongated cæcal *sperm-sac* also opens into the urinogenital sinus, which communicates with the cloaca at the apex of a papilla (Fig. 349). In the Holocephali, the vas deferens forms a large, coiled mass anteriorly, and is connected with the testis by mesenteric folds, but in the absence of a mesonephric part of the epididymis it is not clear how the sperms pass into it: they become aggregated into spermatophores before entering the elongated and septate seminal vesicles. Vestiges of the anterior end or even the whole (Holocephali) of the Müllerian ducts can be recognised in adult Elasmobranchs.

The ovaries and testes of most **Teleosts**, which usually produce an enormous number of generative cells, closely correspond with one another as regards position and the arrangement of their ducts. Dorsal and ventral folds of the peritoneum are developed in connection with the elongated ovary, and these in most cases meet along its outer side, so as to enclose a portion of the cœlome and thus convert the ovary into a hollow sac ("cystoarian" condition), which is blind anteriorly and on the inner, folded walls of which the ova arise. The peritoneal folds are eventually continued backwards to form the oviduct (Fig. 350), which is generally short, and as a rule fuses with its fellow to form an unpaired canal: this opens either by a genital pore (p. 390) between the rectum and the urinary aperture on a level with the integument, or on a papilla, which may become elongated to form a tube or "ovipositor"; or the ducts may communicate with a urinogenital sinus. The testis is elongated, often lobulated in form, and consists of radially arranged tubules or of acini. Its duct has similar relations to those seen in the female, arising, however, not in the form of a simple tube, but as a network of anastomosing canals, which usually open into the posterior end of the kidney-duct.

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[1] The shell-gland secretes the horny material for the egg-case or "purse," which in Plagiostomes is usually produced at its four angles into longer or shorter tendril-like threads; in Cestracion it has a spiral ridge, and in Callorhynchus it is very large and expanded and covered on one side by hair-like processes. In viviparous forms the egg-shell becomes more or less reduced.

Thus the ducts, both of the ovary and testis, correspond to folds of the peritoneum enclosing a cœlomic cavity continuous with that of the gonads, and originate quite independently of the nephridial system. The oviducts must therefore be distinguished from true Müllerian ducts.

In some Teleosts, as in most other Fishes, the ovary is solid and not enclosed in a cœlomic sac, the ova being shed into the body-cavity ("gymnoarian" condition). In the Smelt (Osmerus) and in Mallotus the oviducts ("peritoneal funnels") are not continuous with the ovaries, but have open cœlomic apertures close to the latter, into which the ova pass (cf. Fig. 350, B); while, in other Salmonidæ and, *e.g.*, in the Murænidæ and Cobitis, these peritoneal funnels are shorter, and may even be absent, the ova then being shed into the urinogenital sinus through a paired or single genital pore.[1] It is uncertain whether the latter is the primitive arrangement amongst Teleostei, or whether the peritoneal funnels represent reduced oviducts. In the Eel, a similar reduction of the gonoduct is seen in both sexes.

Hermaphroditism regularly occurs in certain Teleosts (*e.g.* Serranus, Chrysophrys), and has been occasionally observed in some others (*e.g.* Cod, Mackerel, Herring).

Amongst **Ganoids** the female organs of Lepidosteus are formed on the same type as those of the Teleostei. In Amia (Fig. 350, B) and Acipenser each oviduct opens by a wide funnel into the cœlome, but in all Ganoids each oviduct is probably comparable to that of Teleosts, and not to a Müllerian duct. In the male Lepidosteus, Amia, and Acipenser, a series of vasa efferentia pass out from the testis and open into a longitudinal canal from which ducts enter the kidney, and then either communicate with the Malpighian capsules, or else pass directly into the mesonephric duct, which therefore serves as a urinogenital duct (Fig. 351). In Lepidosteus the latter dilates before uniting with its fellow to open into the urinogenital sinus. In Polypterus, there is a special testis-duct comparable to that of Teleosts; it is associated with a network of cavities and opens into the posterior end of the kidney-duct. Except in Lepidosteus, representatives of the oviducts of the female are said to be present in the form of short cœlomic funnels opening into the kidney-ducts.

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[1] Most Teleostei are oviparous, but viviparous forms occur (p. 436). The male Stickleback builds a nest for the protection of the young formed of a hardened secretion (mucin) of the kidney, which thus undergoes a change of function at the breeding-season. In Syngnathus and Hippocampus the young are protected within a pouch on the abdomen of the male, and in the female Solenostoma in a pouch between the ventral fins; amongst Siluroids they are carried within the pharynx in the male Arius, and attached to the soft ventral integument in the female Aspredo.

In the **Dipnoi** (Fig. 352) the elongated gonads are invested with lymphoid and adipose tissue, are closely attached to the outer border of the kidneys, and when ripe become greatly enlarged, so as to embrace the gut ventrally. The oviducts, which correspond to Müllerian ducts, are long and coiled, resembling those of the Amphibia: posteriorly they unite before

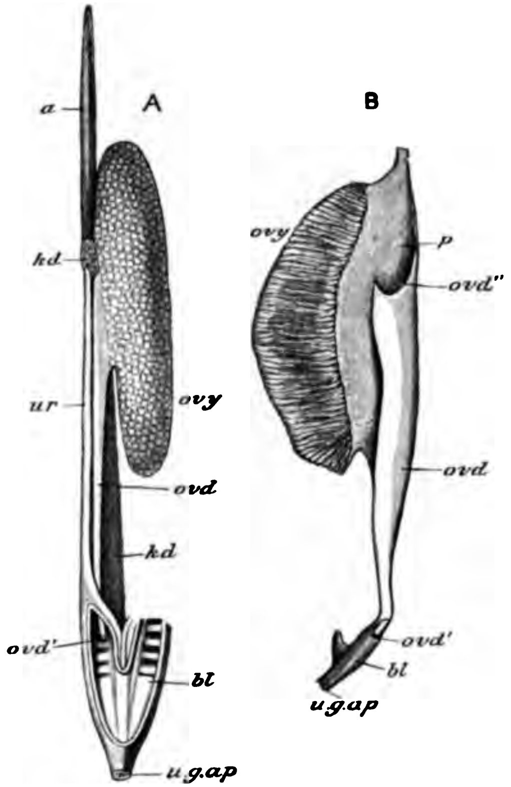

FIG. 350.

FIG. 350.—FEMALE URINOGENITAL ORGANS OF A, LEPIDOSTEUS, AND B, AMIA. (A, after Balfour and Parker; B, after Huxley.)

a, degenerate anterior portion of kidney; *bl*, bladder; *kd*, kidney; *ovd*, oviduct; *ovd'*, aperture of oviduct into bladder, and *ovd''*, its peritoneal aperture; *ovy*, ovary; *p*, peritoneum; *u.g.ap*, urinogenital aperture; *ur*, kidney duct.

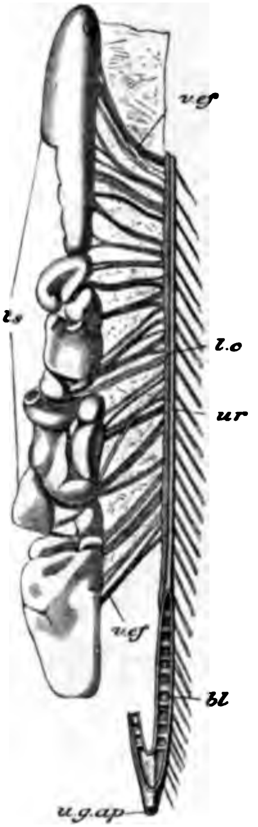

FIG. 351.

FIG. 351.—MALE URINOGENITAL ORGANS OF LEPIDOSTEUS. (After Balfour and Parker.)

bl, bladder; *l.c*, longitudinal canal; *ts*, testis; *u.g.ap*, urinogenital aperture; *ur*, kidney duct; *v.ef*, vasa efferentia.

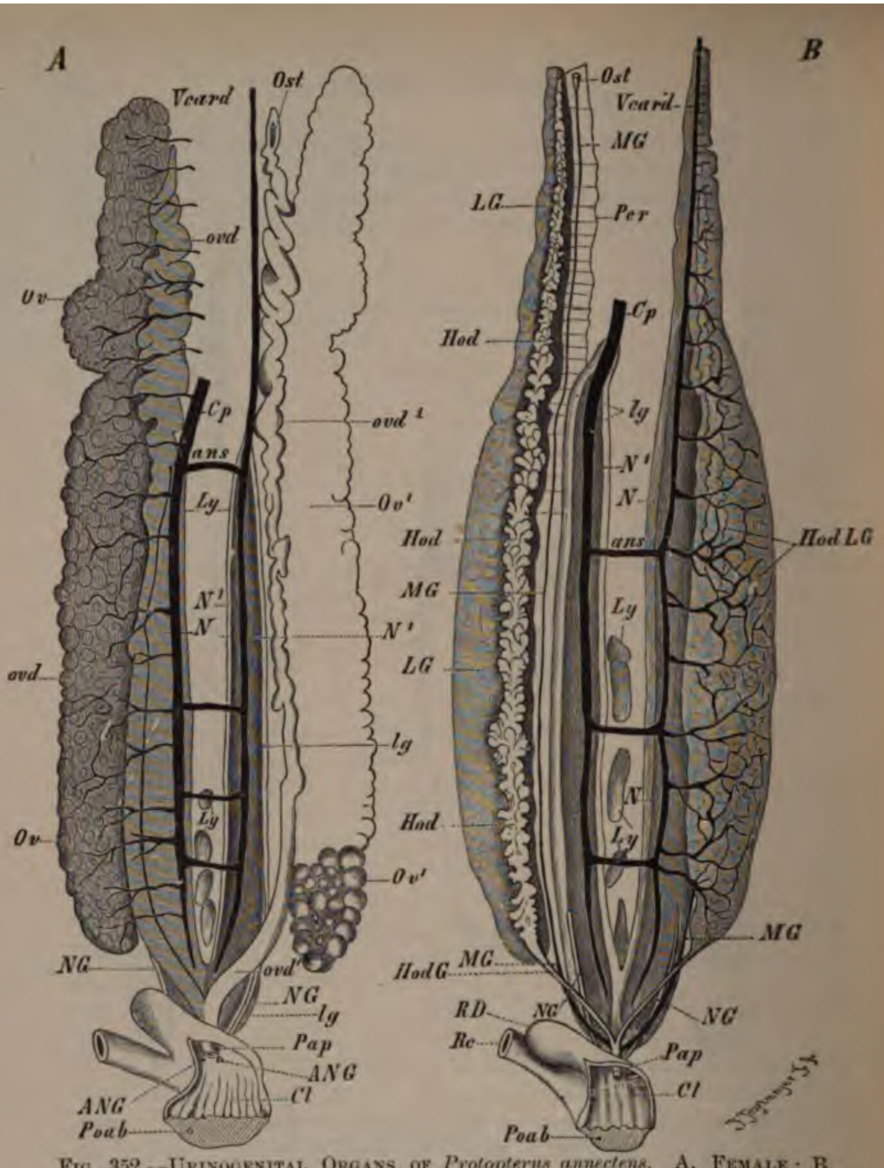

Fig. 352.—Urinogenital Organs of *Protopterus annectens*. A, Female; B, Young Male. (After W. N. Parker, modified after J. Graham Kerr.) The peritoneum (*Per*) is removed on the right side in A, and on the left in B.

In both figures: *Cp*, postcaval vein, connected by transverse anastomoses (*ans*) with the left posterior cardinal vein (*V.card*); *lg*, *ly*, lympathic tissue in connection with the kidneys; *NG*, mesonephric duct; *N*, N^1, kidneys; *Ost*, cœlomic aperture of Müllerian duct; *Poab*, abdominal pore; *Rc*, rectum; *RD*, cloacal cæcum. The veins from the gonads are also indicated.

In A: *ANG*, apertures of kidney ducts into the cloaca (*Cl*); *Ov*, Ov^1, ovaries; *ovd*, *ovd'*, oviducts; *Pap*, genital papilla in the cloaca formed by the fusion of the base of the Müllerian ducts.

In B: *Pap*, urinogenital papilla; *Hod*, testes, with their investment of lymphoid and adipose tissue (*LG*); *Hod.G*, vesicular portion of testis, which unites with its fellow posteriorly, dorsal to which point the posterior ends of the kidneys (epididymes) are also fused together, and are not deeply pigmented, like the rest of the kidney; *MG*, Müllerian duct.

opening into the cloaca, and each communicates anteriorly with the body-cavity by a funnel-shaped aperture. The wall of the oviduct secretes albumen round the eggs as they pass along it.

In Protopterus and Lepidosiren, the greater portion of the testis is composed of numerous sperm-producing ampullæ opening into a longitudinal duct continuous with a cavity in a simplified posterior prolongation of the gonad, in which no sperms are formed, and which converges posteriorly, fusing with its fellow in Protopterus: it serves merely as a duct and as a vesicula seminalis. From the posterior end of this portion a testicular network arises in Lepidosiren, from which about six vasa efferentia pass into the Malpighian capsules of the mesonephros ("posterior epididymis," p. 455), while in Protopterus there is only a single large and irregular vas efferens on either side. Thus the posterior end of the mesonephric duct is urinogenital in function.

In Ceratodus the manner in which the sperms are conducted from the testis to the exterior is not definitely known. The Müllerian ducts in this genus are retained in the adult, and possess a lumen throughout: in Protopterus they undergo further reduction, and apparently the middle part disappears, the posterior end fusing with its fellow and ending blindly at the base of the urinogenital papilla, while in Lepidosiren only the anterior end persists.

Thus a communication between the testis and kidney occurs in Elasmobranchii, certain Ganoidei (Lepidosteus, Amia, Acipenser), Dipnoi, Amphibia, and Amniota, and on the assumption that the condition in Polypterus and Teleostei is a secondary and not a primary one, an attempt to bring these latter into line with the majority of Vertebrates in this respect is represented diagrammatically in Fig. 353.

Amphibians.—The form of the gonads of Amphibia is usually modified in correspondence with the shape of the body. Thus in the Gymnophiona the ovary has the form of a long and narrow band, and the testis consists of a long chain of small bodies united together by a collecting duct (Fig. 354). Each individual portion of the testis of Cæcilians is made up of a double row of rounded capsules in which the sperms are formed, and from which they are passed into a collecting duct, which perforates each portion of the organ. A transverse canal is given off from the free portion of the collecting duct lying between every pair of testis-lobes; this passes towards the kidneys, and opens into a longitudinal canal. From the latter the sperms pass through a second system of transverse canals to the Malpighian capsules, and thence through the urinary tubules into the urinogenital duct.

The male generative apparatus of all Urodela and certain Anura (Bufonidæ) corresponds in the main with that seen in Cæcilians, except as regards the form of the gonads: thus the testis

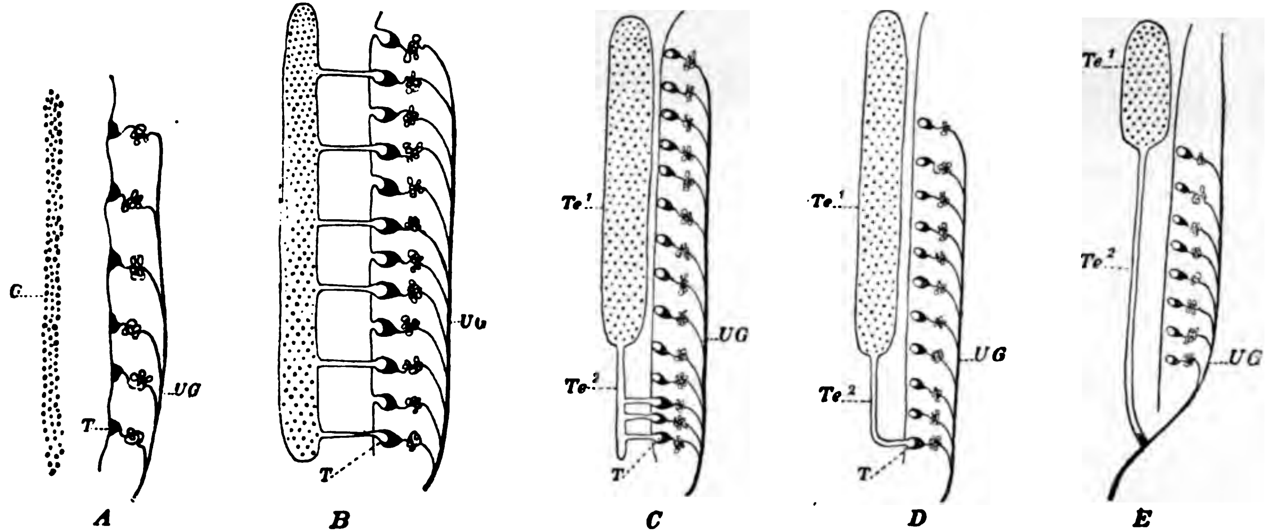

FIG. 353.—DIAGRAMMATIC SKETCH OF THE URINOGENITAL SYSTEM IN CERTAIN FISHES. (After J. Graham Kerr.)

G, germinal area of cœlomic lining; *T*, cœlomic funnels (nephrostomes) of kidney tubules; *Te*^{1}, formative region of testis; *Te*^{2}, vesicular region of testis; *UG*, mesonephric (Wolffian) duct.

A. Hypothetical primitive condition, in which the genital products are shed freely into the general cœlome and carried to the exterior through the nephridial funnels.

B. The portions of cœlome round the nephridial funnels are constricted off from the general cœlome as Malpighian capsules, which still, however, communicate with the general cœlome. The genital portion of the cœlome is also shut off from the general cœlome as the cavity of the testis. The genital cœlome still remains in communication with the cœlome of certain Malpighian capsules hrough transverse channels—the vasa efferentia. *Acipenser* and *Lepidosteus* show an essentially similar distribution of vasa efferentia o this. Anastomoses between the vasa efferentia are omitted in the diagram.

e capsular portions of the cœlome are now completely cut off from the general cœlome. The testis shows a division into two egions, formative and vesicular, and the vasa efferentia have disappeared, excepting a few towards the hind end of the vesicular region (*Lepidosiren*).

The communication of the testis with the kidney-system is reduced to a single vas efferens at the extreme hind end of the vesicular region of the testis (*Protopterus*). In actual fact, the vas efferens communicates with *several* kidney-tubules.

E. Similar to D, but the communication of the vesicular region of the testis has become more direct by a single, wide, tubular channel (*Polypterus*, *Teleostei*).

is either pointed at one or both ends (Fig. 342), or more or less round or oval (Fig. 343, 355).

In Rana (Fig. 355), Bombinator, and Alytes, the vasa efferentia of the testis gradually become more separated from the kidney. In Rana temporaria, the efferent ducts are connected with a longitudinal canal, from which the sperms pass through the so-called ampullæ (*i.e.* Malpighian capsules which have lost their glomeruli) and the transverse canals to the urinogenital duct: in Rana esculenta the efferent ducts open directly into the urinogenital duct, without becoming connected with the urinary tubules, while in Bombinator the greater number of the posterior canals end blindly, only the anterior ones being directly connected with the urinogenital duct.[1]

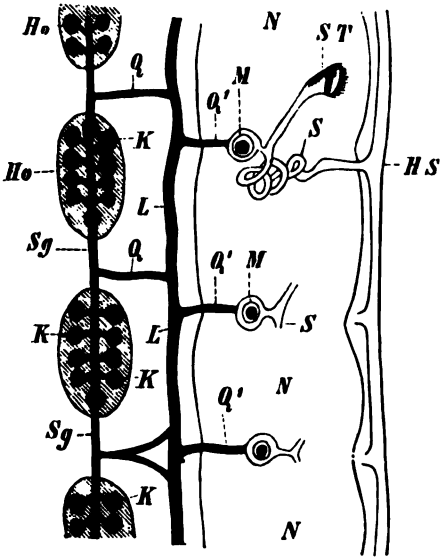

FIG. 354.—DIAGRAM OF A PORTION OF THE MALE GENERATIVE APPARATUS IN THE GYMNOPHIONA.

Ho, testis; *HS*, urinogenital duct; *K*, testicular capsules; *M*, Malpighian capsules; *N*, kidney; *Q*, transverse canals connecting the collecting duct with the longitudinal canal (*L*, *L*); Q^1, second series of transverse canals; *S*, convoluted portion of urinary tubule; *Sg*, collecting duct of testis; *ST*, nephrostome.

Müllerian ducts are always present in a more or less vestigial condition in the male, and lie along the outer border of the kidneys in a similar position to those of the female. They may or may not be provided with a lumen and apertures of communication with the body-cavity and cloaca. A vesicula seminalis may be present on the urinogenital duct (p. 457).

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[1] In Alytes the relations of the generative ducts require further investigation: the efferent ducts at the anterior end of the kidney are said to open into the Müllerian duct.

Hermaphroditism occasionally occurs in the Anura; only one case (Triton tæniatus) is known amongst Urodeles. A body attached to the anterior end of the testis ("Bidder's organ") in various species of Toads contains cells quite similar to young ova, and a similar body is present at the anterior end of the ovary, the cells in which are, however, incapable of ripening. In the males of Pelobates, Bufo, and Rana temporaria, ova are at times developed within the substance of the testis (*hermaphrodite gland* or *ovotestis*), and one testis may even be replaced by a rudimentary ovary: in Rana, the Müllerian duct may then be as well developed as in the female.

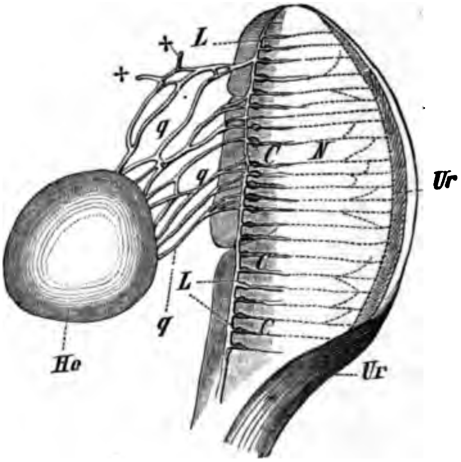

FIG. 355.—TESTIS AND ANTERIOR END OF KIDNEY OF *Rana esculenta*. (Semidiagrammatic.)

Ho, testis; *L*, longitudinal canal of the testicular network, from which the inter-renal network (*C*, *C*) arises; *N*, kidney; *q*, *q*, transverse canals of the testicular network, which give rise to blind processes at † †; *Ur*, urinogenital duct.

The ovaries of Urodela are always formed on a common plan: each consists of an elongated, closed tube, with a continuous lumen. In Anura, on the contrary, the ovarian sac (Fig. 356) is divided up into a longitudinal row of numerous (3 to 20) separate pockets or chambers, on the walls of which the ova are developed and project into the cavity, eventually breaking through into the cœlome. The oviducts open far forwards into the body-cavity by funnel-shaped apertures; they take a tolerably straight course along the outer borders of the kidneys to the cloaca in young animals, but become greatly convoluted and glandular later. A short distance from its termination, each oviduct in Anurans becomes dilated to form a thin-walled sac, in which the eggs, covered by a gelatinous coating from the glands in the wall of the middle part of the oviduct, become collected before oviposition: after again narrowing, it usually opens separately on a papilla on the dorsal wall of the cloaca: in the genera Bufo and Alytes the two oviducts fuse posteriorly into an unpaired canal.[1]

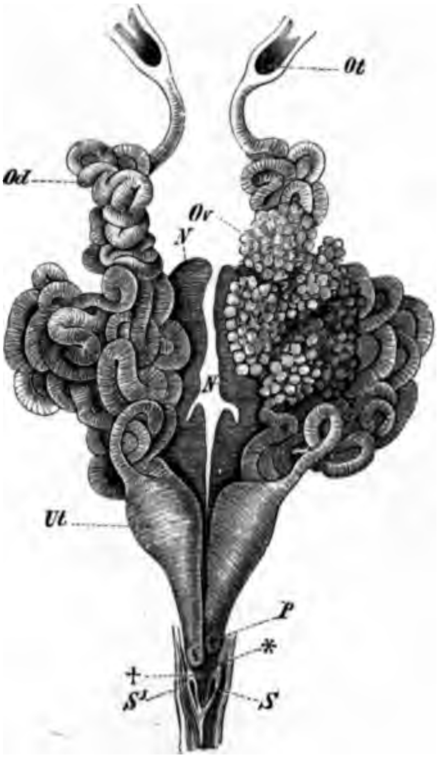

FIG. 356.—URINOGENITAL ORGANS OF A FEMALE *Rana esculenta*. From the ventral side.

N, kidneys; *Od*, oviduct; *Ot*, abdominal aperture of oviduct; *Ov*, left ovary (that of the right side is removed); *P*, opening of oviduct into the cloaca; *S*, *S*¹, apertures of urinary ducts into the cloaca, surrounded by longitudinal folds (*), which are separated by a deep depression (†); *Ut*, the dilated posterior end of the oviduct.

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[1] In Epicrium glutinosum (Gymnophiona) the ripe eggs are very similar to those of Sauropsida: they are exceptionally large (9 mm. long), are of an oval shape, possess a large yolk, and the segmentation is *meroblastic*, and takes place in the oviduct. After fertilisation they become coated with tough albumen in the oviduct, and this is drawn out at the poles into chalazæ, by means of which the eggs are connected together like the beads of a necklace. The eggs are laid in the earth, the mother coiling herself round them.

The cloaca in both sexes of Urodeles is provided with definite integumentary lips, and its cavity is often subdivided by folds. In the female, its side walls enclose numerous tubes, which, during the breeding season, serve as *receptacula seminis*.[1] In the male the lips and dorsal wall of the cloaca include numerous glands, amongst which special pelvic and abdominal portions may be recognised, and which are especially well-developed in the breeding season. These serve to secrete a protective jelly-like mass around the spermatozoa, thus uniting them into packets, or spermatophores. It has been observed in Newts that as the spermatophores are extruded from the cloaca of the male, they become taken up by the female between the lips of the cloaca, so that fertilisation of the eggs takes place before, and not after oviposition, as is the case in Anura.

Fat-bodies (*corpora adiposa*) are present in all Amphibia in connection with the gonads: they are formed of adenoid tissue, fat, and leucocytes, and contain numerous blood-vessels. These bodies have probably an important physiological (nutritive) relation to the gonads: after remaining for months without food, throughout their winter sleep, Amphibians are able as soon as spring arrives to produce thousands of offspring.

Reptiles and Birds.—The essential differences between the urinogenital organs of the Anamnia and Amniota have already been referred to (cf. Fig. 339).

In the Sauropsida, as in other Vertebrates, the form of the gonads is influenced by that of the body: thus in Chelonians they are broad, while in Snakes and snake-like Lizards they are more elongated, and as well as in other Lizards, are asymmetrical, the organ of one side lying more or less in front of that of the other. More room is thus obtained for the development of the ovaries; and, in cases where the eggs are very large, the organs of one side tend to disappear, as in certain Elasmobranchs: in Birds, for instance, the left ovary only is completely developed and functional. In Reptiles the ovaries are penetrated by a highly vascular network of trabeculæ, in the lymph-cavities of which the formation of ovarian follicles takes place.

The oviducts (Fig. 357) possess wide, funnel-shaped, abdominal apertures, and are usually much folded transversely; the right is often longer than the left. Their walls are provided with numerous muscular elements and glands for the formation of the albumen and egg-shell, and they increase in size in the breeding-season. In Birds the right oviduct, as well as the right ovary, becomes more or less completely degenerated, and the left is considerably coiled.

Only slight remnants of the mesonephros and Wolffian duct persist in female Reptiles, and these undergo fatty degeneration. They are arranged in a single asymmetrical row on either side,

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[1] In Salamandra maculata and S. atra the contai [illegible] in their vitality for a year or two.

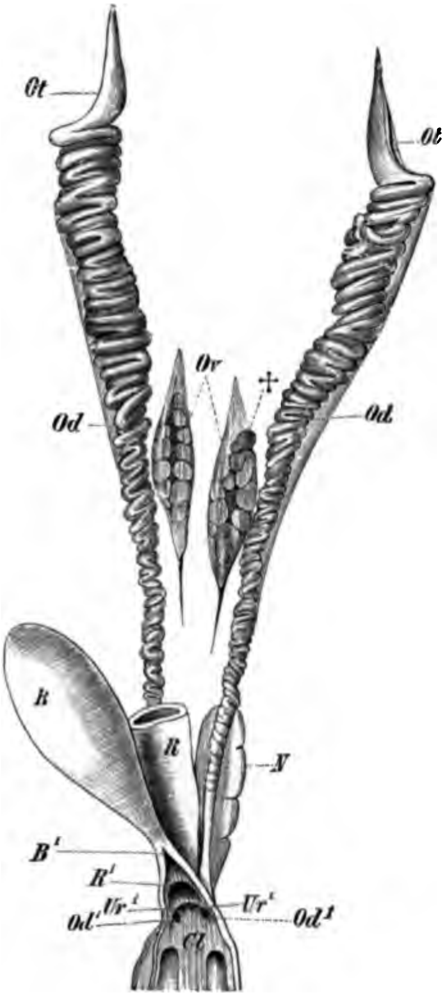

FIG. 357.—FEMALE URINOGENITAL APPARATUS OF *Lacerta muralis*.

B, urinary bladder; B^1, neck of the bladder (cut open); *N*, kidneys; *Od*, oviducts, which open into the cloaca at Od^1; *Ot*, abdominal openings of oviducts; *Ov*, ovaries; *R*, rectum; R^1, opening of rectum into the cloaca (*Cl*); Ur^1, apertures of the ureters into the cloaca; †, remains of mesonephros.

between the oviduct and vertebral column. The vestiges of the Wolffian duct are more marked in female Snakes, Chelonians, and kos than in the majority of Lizards.

The testes of Sauropsida correspond in position with the ovaries, and, like them, increase in size in the breeding-season; in Birds, one is generally larger than the other. They have an oval, round, or pyriform shape (Figs. 346 and 358), and are made up of greatly convoluted seminal tubules connected by fibrous tissue. In Reptiles (*e.g.* Lacerta, Anguis), "yellow bodies," which correspond to adrenals (p. 495), lie along the outer border of the testis, and at this point transverse canals pass out from the testis to the epididymis. The latter consists of greatly convoluted canals, and from it arises the vas deferens (Wolffian duct), which either takes a straight course, or is more or less coiled. In Birds it opens by an independent aperture into the cloaca, while in Lizards it fuses with the ureter shortly before entering the latter.

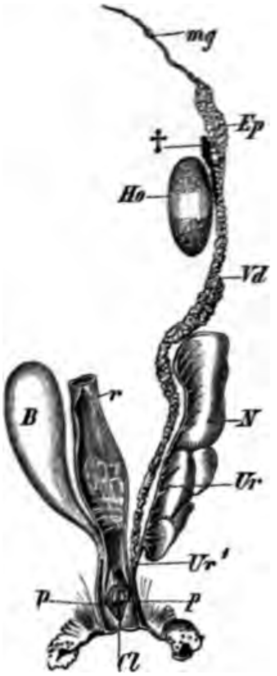

FIG. 358.—MALE URINOGENITAL ORGANS OF *Anguis fragilis*. (After F. Leydig.)

B, urinary bladder; *Ep*, parorchis; *Ho*, testis; *mg*, vestige of the Müllerian duct; *N*, kidney; *p*, common aperture of the ureter (*Ur*, Ur^1) and vas deferens on a papilla on the dorsal wall of the cloaca (*Cl*); *r*, rectum; *Vd*, vas deferens; †, "yellow body" (adrenal).

Remains of the Müllerian ducts are present in the male, corresponding in position with those of the female. Their lumen is not continuous throughout, but the abdominal aperture may remain open (Emys europaea), and exceptionally (*e.g.* individuals of Lacerta viridis) they may be as well developed as in the female.

Accessory genital glands are present in most Reptiles, as in Amphibians, but it is doubtful whether, or to what extent, they are comparable to those of Mammals (p. 484). In Lizards they are well-developed on the dorsal and ventral walls of the cloaca, and their secretion passes into the grooved penes in the male. In Snakes similar glands are present, and in mature Crocodiles odoriferous ("musk") glands open into the cloaca, and are said to be eversible. Accessory genital glands are wanting in Chelonians: in those in which so-called "anal vesicles" are present, they are hydrostatic in function.

Lymphoid organs are present in many Reptiles, here also have a physiological relation to the gen (cf. p. 474). In many Lizards they are large and variously coloured, and lie within the pelvic region; in Snakes they extend along almost the entire body-cavity.

Among Birds, true hermaphroditism has been observed very exceptionally in the Chaffinch. In some cases the ovary may undergo structural changes, and no longer produce ova, the female then taking on certain secondary sexual characters of the male.

Mammals.—In Mammals the generative apparatus no longer extends along the entire body-cavity, as in the lower Vertebrates, but is confined to the lumbar and pelvic regions. Moreover, in correspondence with the close relations which usually take place between mother and embryo (p. 438), there is a much greater differentiation of the generative organs than occurs in lower types. The transition is not, however, a sudden one, for in the lowest Mammals, viz., the Monotremes and Marsupials (Figs. 359 and 360), these organs show many points of resemblance to those of Reptiles and Birds.

In the oviparous Monotremes[1] the left ovary is better developed than the right, and each has the appearance of a bunch of grapes: the cloaca persists, and the oviducts (Müllerian ducts), which in other Mammals become more or less fused with one another proximally, remain distinct throughout, and open into the urinogenital canal anteriorly to the ureters and bladder.

In the higher Mammals the oviducts become distinctly differentiated into three portions,—a *Fallopian tube*, a *uterus*, and a *vagina*. The vagina opens to the exterior (Figs. 339, 360, and 361), while the Fallopian tube communicates with the abdominal cavity by a funnel-shaped aperture which is usually fimbriated and ciliated.

In Marsupials the ovaries vary much in form, and the fusion of the two oviducts is much less marked than in the higher Mammals: in order to trace the gradual differentiation of these parts, their condition in Opossums (Didelphidæ) will first be considered.

A dilated portion of each oviduct (Fig. 360, A), giving rise to a uterus, is plainly distinguishable from the rest, and its narrowed posterior end comes into close contact with its fellow in the middle line. At this point (†) each uterus communicates with the vagina by a distinct *os uteri*. The vagina curves sharply outwards, and, then backwards, opening close to its fellow into the elongated urinogenital canal. The ureters, as in all other Marsupials in which the vaginæ have a similar arrangement, pass between the curved portions of the vaginæ to the bladder.

From the condition of the female generative organs in

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[1] The eggs (usually one in Echidna and two in Ornithorhynchus), surrounded by a thin shell of keratin, have only been found in the left oviduct, in which their early devel [illegible] place.

Didelphys, that seen in other Marsupials may be derived. In Phalangista vulpina and Phascolomys wombat (Fig. 360, B and C)

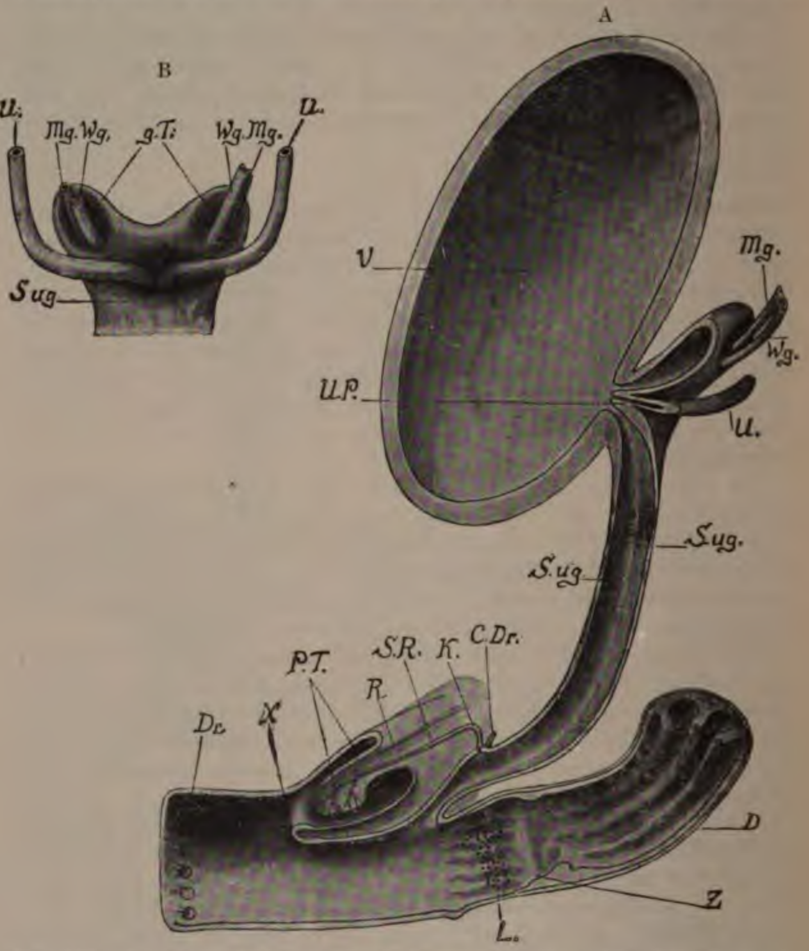

Fig. 359.—A, Diagrammatic Median Section to show the Relations of the Bladder, Urinogenital Canal, and Cloaca in both Sexes of *Echidna aculeata*; B, Diagram of the Anterior Part of the Urinogenital Sinus from the Dorsal Side. (After F. Keibel.)

C.Dr, aperture of Cowper's glands into the urinogenital canal; *D*, rectum; *Dr*, apertures from which project bundles of hair, with sebaceous and sweat glands; *g.T*, genital pouch; *K*, bend in urethral canal; *L*, lymphatic tissue; *Mg*, Müllerian duct; *PT*, preputial pouch and copulatory organ; *S.R*, canal of copulatory organ; *S.ug*, urinogenital canal; *U*, ureter; *U.P*, papilla of ureter; *Wg*, Wolffian duct; *x*, aperture of preputial pouch into cloaca; *Z*, aperture of rectum into cloaca.

the anterior ends of the knee-shaped bends of the vaginæ lie closer together, and begin to extend backwards towards the urino-

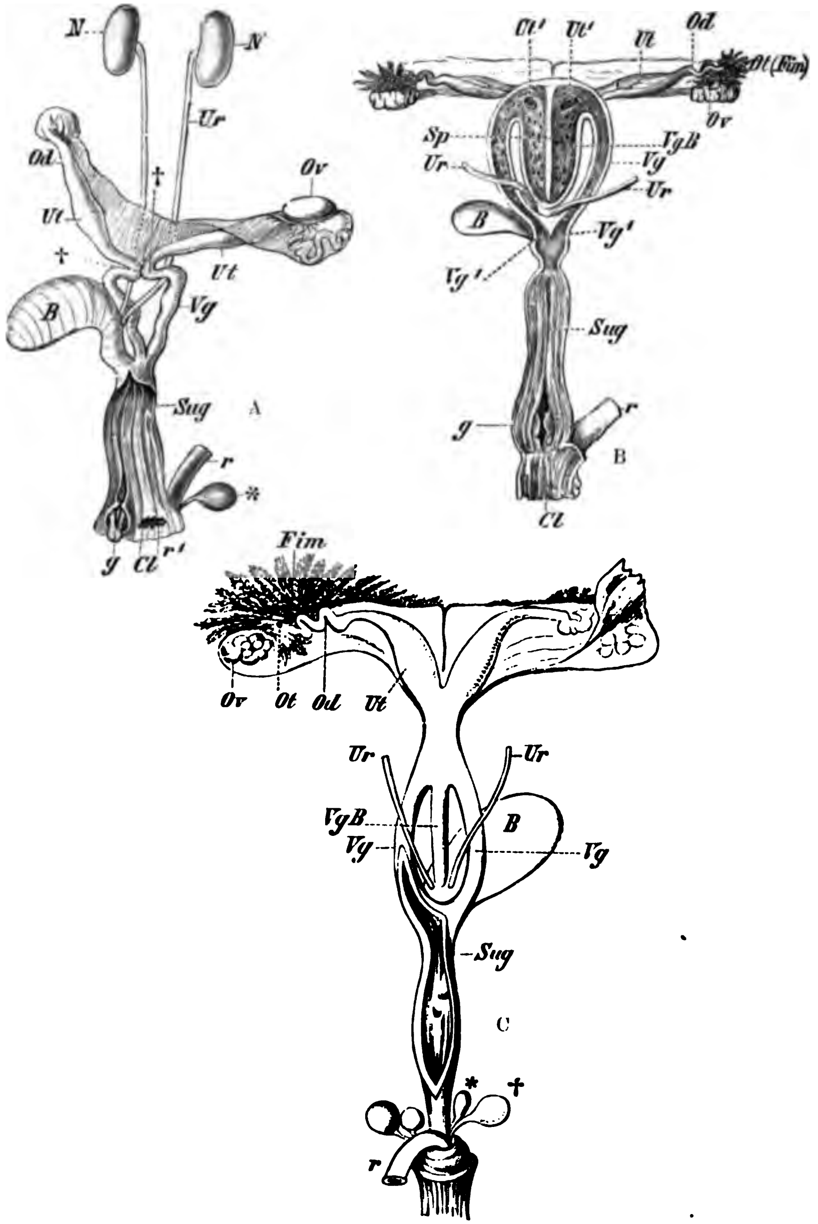

FIG. 360.—FEMALE GENERATIVE APPARATUS OF MARSUPIALS. A. *Didelphys dorsigera* (juv.); B, *Phalangista vulpina*; C, *Phascolomys wombat* (After A. Brass.)

B, urinary bladder; *Cl*, cloaca; *g*, clitoris; *N*, kidney; *Od*, Fallopian tube, and *Ot* (*Fim*), its abdominal opening; *Ov*, ovary; *r*, rectum, which opens at r^1; *Ur*, ureter; *Ut*, uterus; Ut^1, openings of uteri into the vaginal cæcum, *VgB*; Vg^1, apertures of vaginæ into the urinogenital canal (*Sug*); *, †, rectal glands; †, bend between uterus and vagina.

genital canal, the septum between them disappearing at the same time. A *vaginal cæcum* is thus formed: this may become more elongated, and finally extend backwards so as to meet the anterior wall of the urinogenital canal, into which it may in some cases eventually open by the formation of a so-called *third vagina*, as, *e.g.*, in certain species of Macropus and Halmaturus. The anus and urinogenital apertures are surrounded by a common sphincter.

In nearly all the placental Mammals (Monodelphia) the posterior portions of the Müllerian ducts become fused to form an unpaired vagina, and a definite cloaca exists only in the embryo; but even in the adult, the anus and urinogenital aperture may in certain cases (*e.g.* amongst Rodents) be enclosed by a common fold of the integument as in Marsupials, and a median septum is sometimes present in the vagina distally, indicating its primarily double nature. The uterine portions of the oviducts may also fuse with one another to a greater or less extent, and thus the most various forms of uteri result (Fig. 361, A to D), viz.—*uterus duplex*, with two ora uterorum (most Rodents), *uterus bipartitus* and *uterus bicornis*, double in part only and with one os uteri (Carnivores, most Ungulates), and *uterus simplex* (Primates). In the last-mentioned form the primitively paired condition of the Müllerian ducts is seen only in the Fallopian tubes, which vary much in form. The ureters, unlike those of Marsupials, always pass to the outer side of the genital passage, the vagina being single.

The urinogenital canal may, as in Marsupials, be of considerable length (*e.g.* amongst Rodents), and a fold of the mucous membrane (*hymen*)[1] is often present where the vagina opens into it. On the ventral wall of the urinogenital canal, the *clitoris* (p. 487) is situated. In both male and female the space between the urinogenital aperture and the anus is known as the *perinæum*.

The ovaries of monodelphous Mammals are usually small, and rounded or oval in shape, their surface being either smooth, irregular, or furrowed. The point at which the nerves and vessels enter is not covered by peritoneum, and is called the *hilum*. Various differences are seen as regards the relations of the peritoneum to the ovary, and from a simple investment on the ventral side, the organ hardly sinking into the peritoneum at all (*e.g.* Rabbit, Cat), all stages occur up to its complete investment so as to form an ovarial sac.

Remains of the mesonephros, known as the *parovarium*, are present in the neighbourhood of the ovary, oviduct, and uterus. These usually consist of small cæcal tubes, forming a network, which are connected together by a collecting duct. In cases

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[1] A similar fold, closing the apertures of the oviducts in the immature condition, is present in Elasmobranchs.

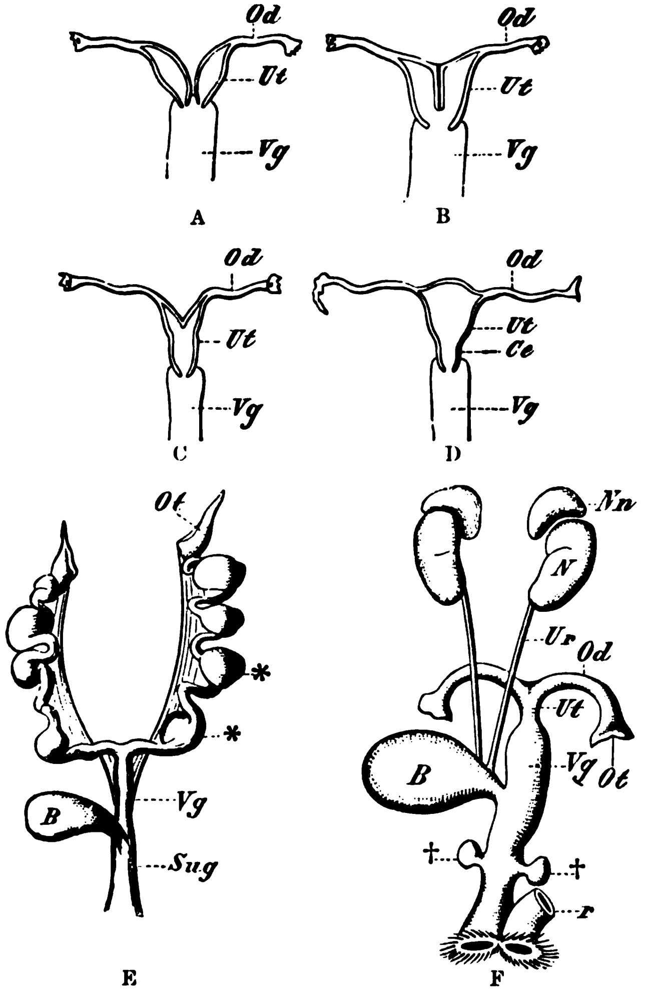

FIG. 361.—VARIOUS FORMS OF UTERI. A, B, C, D, diagrams showing the different stages in the fusion of the Müllerian ducts: A, uterus duplex; B, uterus bipartitus; C, uterus bicornis; D, uterus simplex; E, female urinogenital apparatus of *Mustelina*, containing embryos (* *) in the uterus; F, ditto of Hedgehog (*Erinaceus*).

B, urinary bladder; *Ce*, cervix uteri; *N*, kidney; *Nn*, adrenal; *Od*, Fallopian tube; *Ot*, abdominal aperture of Fallopian tube; *r*, rectum; *Sug*, urinogenital canal; *Ur*, ureter; *Ut*, uterus; *Vg*, vagina; †, †, accessory glands.

where the Wolffian duct persists in the female, it passes from the parovarium to the urinogenital canal, and is spoken of as *Gärtner's duct* (Fig. 339, H).

A fold of the skin of the abdomen forming a *pouch* or *marsupium* is pre[illegible]na and to a greater or less extent in

Marsupials[1] (p. 35): in the former this serves to protect the egg, and in the latter the young, which are born in a very unripe condition, thus rendering possible a longer connection between the mother and embryo during lactation. The aperture of the marsupial pouch opens anteriorly or posteriorly, according to the mode of life of the animal, and is provided with a sphincter muscle capable of closing it. In Marsupial embryos the margins of the lips become partially fused secondarily and temporarily to form a suctorial mouth, by means of which the young, many of the organs of which are still in a "larval" condition, become attached to the teats (cf. p. 438).

In male Mammals, the testes arise in the same relative position as the ovaries of the female. The ovary, however, does not become shifted further backwards than the pelvis in the course of development; but the testis may pass out of the abdomen through an *inguinal canal* into a purse-like outgrowth of the integument in the inguinal region called the *scrotal sac*, which is lined by a continuation of the peritoneum, the *tunica vaginalis* (p. 362). The two scrotal sacs may remain separate, or unite to form a *scrotum*: in Marsupials this is situated in front of, and in placental Mammals behind the penis. If the inguinal canals remain widely open, the testes may be withdrawn periodically into the abdomen (as *e.g.* in Rodentia and Insectivora, in which they only descend at sexual maturity): this is effected by means of the *cremaster muscle*, a more suitable name for which would be the *levator* s. *retractor testis*. This muscle is a continuation of the fibres of the internal oblique and transversalis, or of the latter only, and corresponds to the "compressor mammæ" of female Marsupials. When the inguinal canals become reduced (as *e.g.* in Man) the testes remain permanently in the scrotum. In many Mammals, however (*e.g.* Mono-

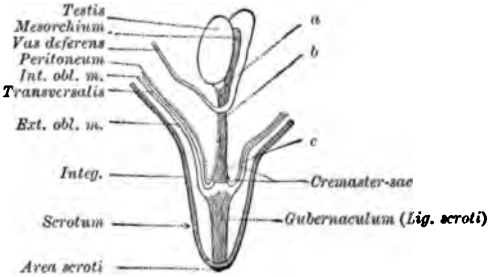

FIG. 362.—DIAGRAM OF THE PARTS CONCERNED IN THE DESCENT OF THE TESTIS. (After M. Weber.)

a, ligamentum testis; *b*, ligamentum inguinale; *c*, muscular conus inguinalis.

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[1] Traces of the marsupial folds occur in young [illegible] various male Marsupials, and indications of a Marsupial app[illegible] described in several of the higher Mammals.

tremes, most Edentates, Hyrax, Elephant), the testes are retained within the abdomen.

Originally, the descent of the testes did not occur until sexual maturity in all cases, but in many Mammals (*e.g.* Marsupials, Ungulates, Carnivora, Primates) the process has gradually become shifted backwards ontogenetically to earlier periods, so that the formation of the scrotum takes place independently in the embryo in the form of the external genital folds, from which also, in the human female, arise the "labia majora" of the vulva.[1]

The testes are smooth, and somewhat oval in form; their relative size varies in different Mammals, and they may become periodically enlarged at the breeding season (*e.g.* Rodents and Insectivores); they are covered by a fibrous investment (Fig. 363), from which processes (trabeculæ) usually extend inwards. Thus the seminal tubules become separated into definite, lobed masses, and a sort of lattice-work is also formed (corpus Highmori) by means of which the elements of the vasa efferentia pass to the epididymis. In the latter the seminal tubules become rounded off to form the so-called *coni vasculosi*, and these are connected together by a collecting duct, the *vas epididymitis*. The vas deferens arises from the last conus vasculosus, and gives rise towards its distal end, shortly before it opens into the urinogenital sinus close to an elevation, the *colliculus seminalis*, to glandular outgrowths (*vesiculæ seminales*), which may attain a relatively enormous size (Fig. 364).

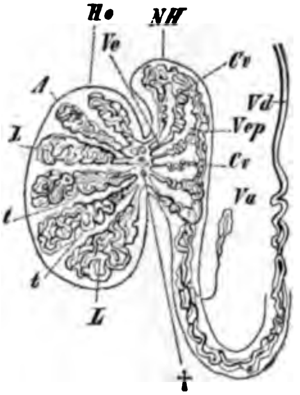

FIG. 363.—DIAGRAMMATIC SECTION OF THE TESTIS OF A MAMMAL.

A, tunica albuginea of the testis, which gives rise to the trabeculæ (*t*, *t*) and the corpus Highmori (†); *Cv*, coni vasculosi, which are connected together by the collecting duct, *Vep*; *Ho*, testis; *L*, *L*, coils of the seminal tubules; *NH*, epididymis; *Va*, vas aberrans; *Vd*, vas deferens; *Ve*, vasa efferentia (rete testis).

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[1] "Labia majora" also occur in certain other Primates, but in most Monkeys "labia minora" [illegible] ent bounding the vulva, and these belong morphologic[illegible] to the scrotal folds.

From this point to its termination at the apex of the penis, the seminal canal is spoken of as the *ductus ejaculatorius.*

In many Mammals vestiges of the Müllerian ducts are present in the male, and open into the urinogenital sinus. In Man, only the posterior end of the ducts remain in the form of an unpaired vesicle (*uterus maculinus*), which lies embedded within an accessory genital gland, the *prostate.*

Accessory genital glands (Fig. 364), certain of which have just been referred to, are present in all Mammals, but vary much in number, form, and relative size. They may be classified as follows :—

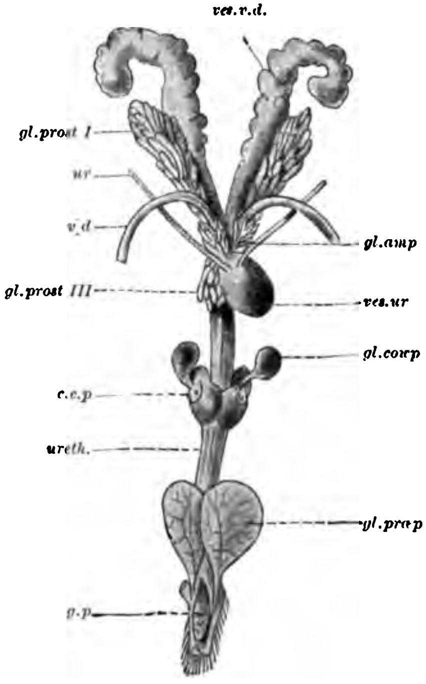

Fig. 364.—Urinogenital Canal and Accessory Genital Glands of a Male Mouse (*Mus musculus*) × 2. (After M. Rauther.)

c.c.p, corpus cavernosum of the penis ; *gl.amp*, ampullary glands : *gl.cowp*, bulbo-urethral (Cowper's) glands ; *g.p*, apex of penis, seen through a slit made in the prepuce ; *gl.præp*, præputial gland ; *gl.prost I*, *prost III*, prostate—the posterior and dorsal portion is hidden ; *ur*, ureter ; *v.d*, vas deferens ; *ves.ur*, urinary bladder ; *ureth*, urethra ; *ves.v.d*, vesiculæ seminales.

I. *Glands arising from the seminal duct.* A. *Ampullary glands*, situated in an ampulla-like enlargement of the seminal duct or embedded in the latter : they are present, *e.g.*, in the Shrew, Ruminants, and certain Carnivores and Rodents ; in many of the last-mentioned Order they are greatly developed. B. *Vesiculæ seminales*, opening into the ductus ejaculatorius together with the seminal duct: they are usually large, saccular, and tubular structures, and occur in certain Rodents, Insectivores, and Bats, and in Sirenians, Elephants, Ungulates (especially Perissodactyles) and Primates.

II. *Glands arising from the urinogenital canal.* A. *Prostate glands*, fully developed in the male only, enclosed by smooth muscles, and sometimes more or less distinctly subdivided into two or three lobes. The prostate is wanting only in Monotremes, Marsupials, Edentates, and Cetaceans. A median sac, opening into the urinogenital canal, is surrounded by the prostate, and the degree of its development exhibits considerable variation. It is usually described as the *vesicula prostatica* or *uterus masculinus*, and in most cases (not, *e.g.*, in Lepus) corresponds to the fused bases of the Müllerian ducts: a more appropriate name would therefore be *vagina masculina*. B. *Urethral glands*, present in both sexes in the form of scattered glands, and more definite and localised bulbo-urethral or *Cowper's glands*, known in the female as the *glands of Bartholini.* These are phylogenetically the oldest glandular appendages of the urinogenital canal. The scattered glands in some cases are abundant, and in others (*e.g.* Canidæ) are wanting: Cowper's glands are, with few exceptions (*e.g.* Dog, Bear, aquatic Mammals), of constant occurrence and position: they are surrounded by striped muscle.

III. Glands of the external genital organs and inguinal region (*preputial*, *inguinal*, and *anal glands*). These are epidermic structures, and are derivable from sebaceous glands or sweat-glands (cf. p. 33).

There seems to be no doubt that the secretions of the prostate, ampullary glands, and seminal vesicles have an important relation to the vitality and fertilising power of the spermatozoa, and a high degree of fertility is usually seen in those animals in which these glands are most markedly developed.[1] The secretions of the preputial, inguinal, and anal glands, in addition to protecting the surface of the skin around the urinogenital and anal apertures, is doubtless of secondary sexual importance, owing to the production of odoriferous substances.

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[1] In many Mammals (*e.g.* Rodents, Insectivores) these glands have also another function. Their coagulated secretion forms a kind of "stopper" for closing the vagina and thus ensuring fertilisation. In certain Bats the mucous membrane lining the neck of the uterus becomes modified directly after copulation, and together with the secretion of the accessory genital glands closes the canal and protects the mass of sperms until the following spring, when fertilisation of the ova takes place: it has been shown that the spermatozoa may thus retain their vitality within the uterus for eight months. In some cases the secretion in the vagina originates from the accessory genital glands of the male.

Copulatory Organs.

Various forms of copulatory organs, morphologically distinct from one another, occur amongst Vertebrates.

In male **Elasmobranchs**, an apparatus consisting mainly of a specially modified portion of each pelvic fin (*clasper* or "*mixopterygium*") serves this purpose (Fig. 365). It consists of a varying number of more or less calcified cartilages, covered by skin and muscles, which are movable upon one another, and most of which are derivatives of the main and lateral fin-rays: it is provided with a channel along the inner side, and becomes separated from the fin itself in varied degrees in different forms. Its apex is usually naked, but may be provided with one or more movable spines, which in the Spinacidæ consist of a curious tissue ("chondrodentin"). These claspers are inserted, in a closed condition, into the cloaca of the female, and thence into the oviducts; they are then opened out by means of special muscles, and the seminal fluid flows along their channels into the distended oviducts. In connection with this apparatus there is a gland (p. 19) surrounded by muscular fibres, which is formed as an involution of the outer integument and consists of branched tubes.

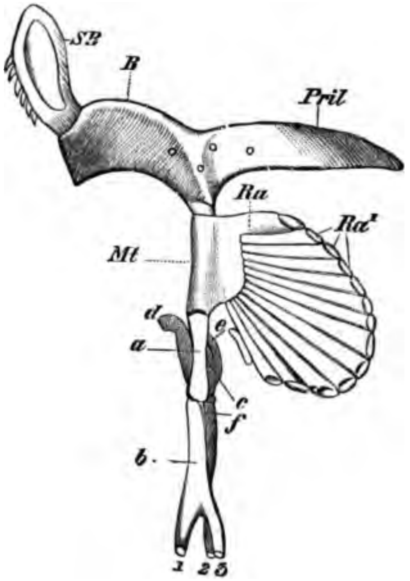

FIG. 365.—PELVIC ARCH WITH SKELETON OF PELVIC FIN AND CLASPERS OF A MALE *Chimæra monstrosa*. (After Davidoff.) Ventral view.

B, pelvic arch with iliac process, *Pril*; *Mt*, basipterygium; *Ra*, *Ra*^{1}, radii of fin; *SB*, anterior clasper; *a—f*, 1—3, various segments of the posterior clasper.

In addition to pelvic claspers essentially similar to those of other Elasmobranchs (the distal part in Chimæra being subdivided and covered with numerous dermal denticles) the Holocephali possess a pair of curious *anterior claspers* (Fig. 365), which are protruded from a shallow pouch situated in front of the pelvic fins; each of these consists of a plate covered with dermal denticles, and in Callorhynchus a grooved structure is present in addition. There is also a knob-like organ, usually known as the *frontal clasper*, on the upper surface of the head (Fig. 66).

Amongst **Amphibians**, the very muscular cloaca in the Gymnophiona can be extruded to a length of 5 centimetres, and thus serves temporarily as a kind of copulatory organ.

Two kinds of copulatory organs are found in **Reptiles**, the one being seen in Lizards and Snakes, and the other in Chelonians and Crocodiles. In the former there are two copulatory sacs or *penes* lying outside the cloaca, under the skin at the root of the tail, and these can be everted and protruded through the vent, and again withdrawn by means of a muscle inserted into the blind end of the sac (Fig. 366). In its everted condition, a spiral furrow extends along each sac down which the seminal fluid passes. These organs, which show no cavernous structure, are also represented in the female, in which, however, they are much smaller.

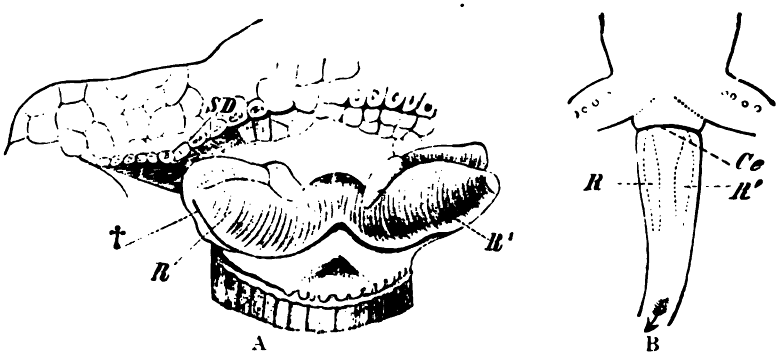

FIG. 366.—COPULATORY ORGANS OF *Lacerta agilis*. (After F. Leydig.) In A they are shown everted, and in B their position in the retracted condition is indicated by dotted lines extending backwards from the vent.

Ce, vent; *R*, *R*^{1}, penes; *SD*, the so-called femoral pores (see p. 23); †, spiral furrow.

In Chelonians and Crocodiles the penis is single, and corresponds to a thickened portion of the anterior lip and ventral wall of the cloaca (Figs. 367, 368, A). It consists of fibrous and cavernous (erectile) tissue and is protrusible, and definite protractor and retractor muscles occur in Chelonia similar to those in Ratite Birds. In the female it is represented by a smaller *clitoris*. The penis bifurcates proximally, and its distal tongue-shaped portion ends freely; a longitudinal groove extends along the upper surface, at the proximal end of which the vasa deferentia open. In Crocodiles the free portion is relatively longer and the groove deeper than in Chelonians.

In many **Birds** a copulatory organ is present, formed on a similar plan to that of Crocodiles. It is well developed amongst the Ratitæ and Lamellirostres, and in many other Birds can be recognised in a rudimentary condition. In Struthio it resembles that of the Crocodile, except that the distal free portion is longer; it is grooved above, encloses cavernous tissues, and is supported by a fibrous body, bifurcated at the base. In Dromæus and Rhea there is an aperture at the apex of the penis leading into an elongated and curved blind sac, in which is a furrow, lined by cavernous tissue, continuous with the groove on the dorsal side of the organ. In the Duck and Swan the spiral penis is essentially similar to that of Dromæus and Rhea. The absence of the blind sac in the Ostrich is probably a secondary modification. A clitoris is present in the female of the above-mentioned Birds.

The penis of **Monotremes** may be best understood by imagining a hypothetical form intermediate between it and that of Crocodiles and Chelonians (Figs. 368, B). We must suppose that a sac-like outgrowth into which the ureters and vasa deferentia open has become developed from the ventral cloacal wall at the base of the penis, the groove in which has become converted into a canal. The Monotreme condition is reached by the sac elongating to form a *urinogenital canal*, into the distal end of which the urinary and genital ducts and the bladder open (C, D). The penis consists of an unpaired fibrous body enclosing the seminal canal, and is only loosely surrounded by the mucous membrane of the cloaca, so that it can be protruded from and retracted into a sheath. In Echidna, cavernous tissue is present in the apex or *glans*; and in Ornithorhynchus the apex is bifurcated and covered with soft spines, the seminal canal or urethra opening in each case by numerous fine canals situated on papillæ. A clitoris is present in the female of all Mammals.

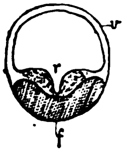

FIG. 367.—TRANSVERSE SECTION OF THE CLOACA OF A CHELONIAN. Slightly diagrammatic. (After Boas.)

f, fibrous body: *r*, seminal furrow, bounded by cavernous issue; *v*, wall of cloaca.

In **Marsupials** (Fig. 369, A), the penis-sheath opens on to the surface of the body, below the anus; the opening of the urinogenital canal into the cloaca has become closed, and is continuous

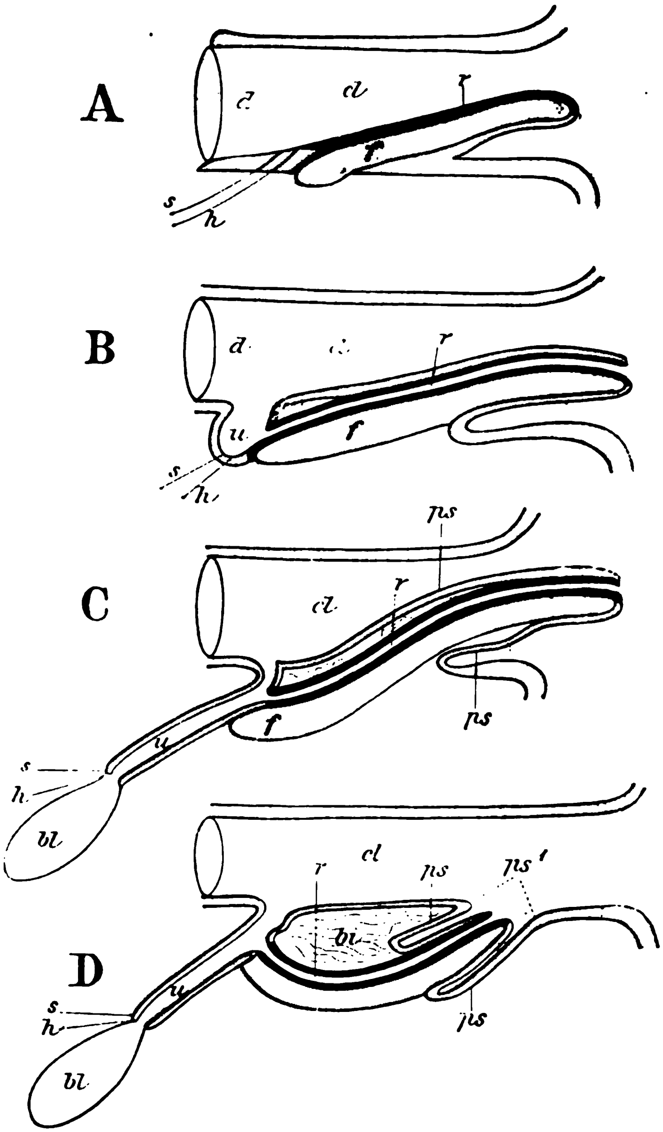

FIG. 368.—DIAGRAMMATIC LONGITUDINAL SECTIONS OF THE POSTERIOR PART OF THE RECTUM, THE CLOACA, AND THE COPULATORY ORGANS OF VARIOUS VERTEBRATES. (After Boas.) The relative positions of the ureter and vas deferens are indicated although not situated in the median line.

A, *Crocodile*; B, hypothetical form between A and C; C, *Monotreme* (penis extruded); D, *Monotreme* (penis [illegible]

bi, connective tissue; *bl*, urinary bla [illegible] ctum; *f*, fibrous body (corpus cavernosum); *h*, ur [illegible] perture of the sheath; *r*, seminal furrow [illegible] as deferens; *u*, urinogenital canal.

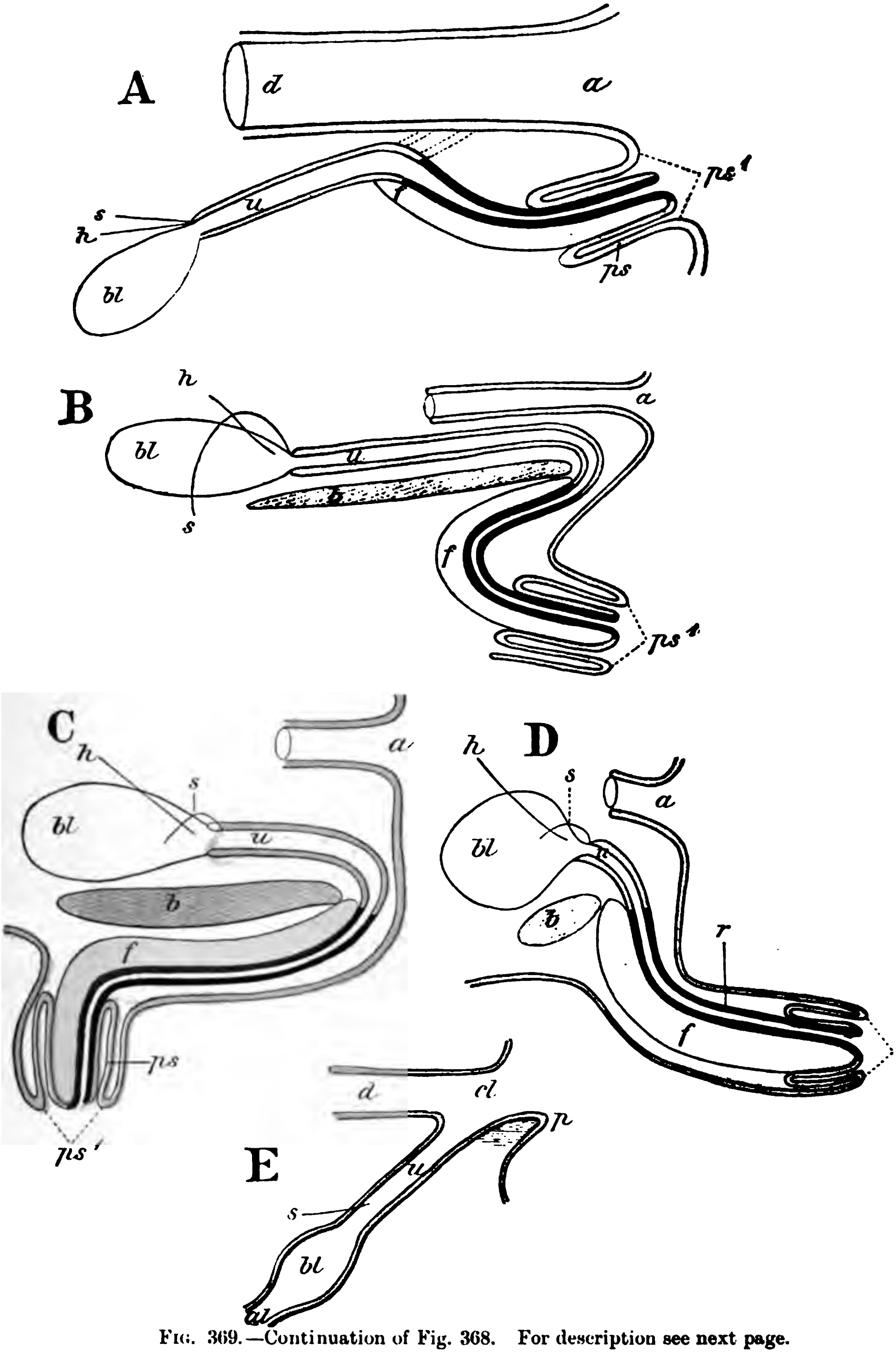

FIG. 369.—Continuation of Fig. 368. For description see next page.

FIG. 369.—CONTINUATION OF FIG. 368.

A, *Marsupial* (very diagrammatic, for comparison with Fig. 368, C; the obliterated opening of the urinogenital canal into the cloaca is indicated by dotted lines); B, *Rodent*, (*Cœlogenys paca*); C, *Ape* (*Cercopithecus*): in most placental Mammals the apex of the penis is not pendulous; D, *Man*; E, *Human fœtus*.

Additional letterings: *a*, anus; *al*, stalk of allantois; *b*, pelvic symphysis; *p*, genital prominence which gives rise to the penis or clitoris.

with the urethra of the penis. The fibrous body is paired, and both it and the walls of the penial urethra are composed of cavernous tissue. Both penis and clitoris are frequently bifurcated at the apex.

Amongst the **Eutheria** the penis of Rodents (Fig. 369, B) and Insectivores comes nearest to that of Marsupials. The paired fibrous body (*corpus cavernosum*) bifurcates proximally to form two crura, which are nearly always attached to the ischia. The opening of the penis-sheath gradually becomes further separated from the anus, and is situated more on the ventral side of the body (cf. B and C), the penis itself lying horizontally along the abdomen. In Primates the organ becomes more or less free from the body-wall, and either its distal end (Apes, C), or the whole of it (Man, D), is pendulous, and the sheath forms a double tube-like investment over the glans—the foreskin or *prepuce*, enclosing sebaceous (preputial) glands.

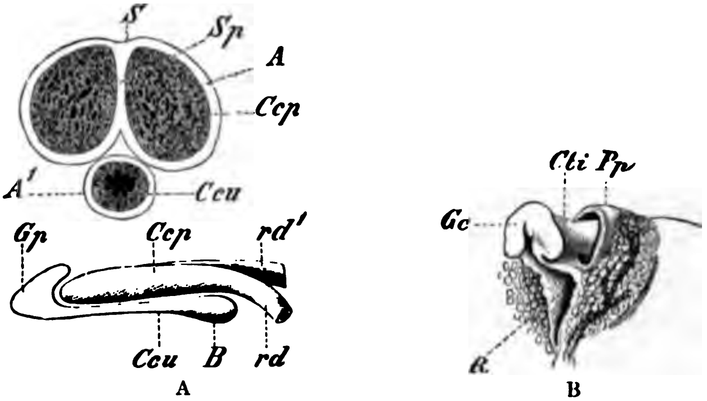

FIG. 370.—A, SEMIDIAGRAMMATIC FIGURE OF THE HUMAN PENIS. (In transverse section and from the side). B, CLITORIS OF A MONKEY (*Cebus capucinus*).

A, albuginea penis; *A*¹, albuginea urethræ; *Ccp*, corpus cavernosum; *Ccu*, corpus spongiosum, which gives rise to the glans penis at *Gp*, and forms an oval enlargement (bulbus) at *B*; *Cli*, clitoris, with its ventral furrow (*R*), glans (*Gc*), and prepuce (*Pp*); *rd*, *rd*¹, crura of the corpora cavernosa; *S*, sulcus dorsalis penis; *Sp*, septum between the two corpora cavernosa.

In the course of development, the penis of Marsupials and

Placental Mammals passes through stages which resemble successively those which are permanent in Crocodiles and Chelonians and in Monotremes. It arises from a "genital prominence" on the ventral wall of the cloaca. A channel passes along the border facing the cloaca to the opening of the urinogenital sinus: this condition is usually retained throughout life in the case of the clitoris, while in the male (and occasionally in the female also[1]) the groove becomes closed to form a canal continuous with the urinogenital canal or urethra, which is thus considerably lengthened. In addition to the paired, erectile corpora cavernosa there is a median *corpus spongiosum* or *corpus cavernosum urethræ* in connection with the penis (Fig. 370): corpora cavernosa are also present in the clitoris, and the corpus spongiosum is represented by the so-called *bulbi vestibuli* of the vulva.

In many Mammals a bone (*os penis*) becomes developed in the septum between the corpora cavernosa (*e.g.* many Monkeys, Rodents, Bats, Carnivores, Whales, Lemurs, Apes). In some there is also a bone or cartilage in the clitoris. The penis may bear horny papillæ and even calcified plates and spines (*e.g.* certain Rodents), and the glans is provided with a special kind of tactile corpuscles.

(For the glands of the external genital organs, cf. p. 484).

ADRENAL BODIES[2]

The adrenals are so called owing to the fact that they are usually situated in close proximity to the kidneys, right and left of the vertebral column. Hence they are usually treated of in connection with the urinogenital organs—a procedure which is only justified by the difficulty of knowing in what other connection to describe them: they have no organic or genetic relation to these organs.

Both morphologically and developmentally the adrenals consist of two distinct parts, one of which arises from the cœlomic epithelium and the other in connection with the rudiments of the sympathetic nervous system; thus both mesoderm and ectoderm take part in their formation.

The constituents formed from the splanchnopleuric cœlomic epithelium originate in the form of numerous epithelial buds or ridges at the dorsal margin of the base of the mesentery, which may extend along the whole trunk and are primarily bilaterally symmetrical: they constitute the bodies which in the lower Vertebrates are known as the *interrenal organ*, and in higher forms (Mammals) correspond to the so-called *cortex* of the adrenals. The ectodermic portion arises at an early stage from the undifferentiated rudiments of the sympathetic ganglia (or from these and the chromaffin cells, cf. p. 247), and in lower Vertebrates the resulting structures are spoken of as the *suprarenal organ*, which corresponds to the *medulla* of the adrenal in Mammals. The original distinction of these two components is plainly retained in the lower Vertebrates throughout life, their union in the higher types being of a secondary nature.

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[1] The formation of a complete canal in the clitoris (*e g.* in many Insectivores, Rodents, and Lemurs) results in an entire separation of the urethra from the urinogenital canal, so that the latter is no longer concerned with the passage of the urine.

[2] The term *adrenal* body is here used to include the two primarily distinct *interrenal* and *suprarenal* organs as described in the text, so as to prevent the confusion arising by the use of "adrenal" and "suprarenal" as synonymous terms.

Amongst **Cyclostomes**, the interrenal organ consists in the Lampreys of small clusters of epithelial cells along the cardinal veins, into the walls of which they extend as far as the lining epithelium; they are most markedly aggregated in the fatty tissue lying between these veins and the aorta, and are also present along the renal vessels. The suprarenal organ also consists of epithelial tissue the constituents of which have the characteristics of chromaffin cells: it extends along the parietal arteries arising from the aorta, following their dorsal and ventral branches in the body-walls, and also occurs between the aorta and cardinal vein of either side, extending into the walls of the latter. The groups of these cells may give rise to clusters (*e.g.* on the sinus venosus) resembling those of Elasmobranchs and Amphibians; and in many places elements of the interrenal organ may occur amongst them, without, however, uniting with them. Both interrenal and suprarenal extend into the tail, mainly along the caudal artery and vein. In the head the suprarenal alone is present, and is situated along the jugular and parietal vessels, while in the neighbourhood of the pronephric rudiments the interrenal alone is found.

In **Elasmobranchs** the two constituents also remain perfectly distinct (Figs. 371 and 372). The suprarenals extend along the whole body-cavity, and in Acanthias, Mustelus, and Galeus occur regularly in every segment, while in others a fusion may take place in many parts, resulting in an apparent reduction in number (Rays). Their connection with the sympathetic ganglia is a very intimate one. The fully-formed interrenal bodies consist of more or less distinctly paired masses composed of cellular tubes or cords and of blood-vessels, and may be connected with one another in a longitudinal direction and also left and right. Fatty particles enclosed within the cells give the organ a yellowish colour.

In **Teleosts** the suprarenals and interrenals are usually interspersed amongst one another, and lymphoid cells always occur in their neighbourhood. The suprarenals are related to the walls of the cardinal veins—especially the larger, right cardinal—and are

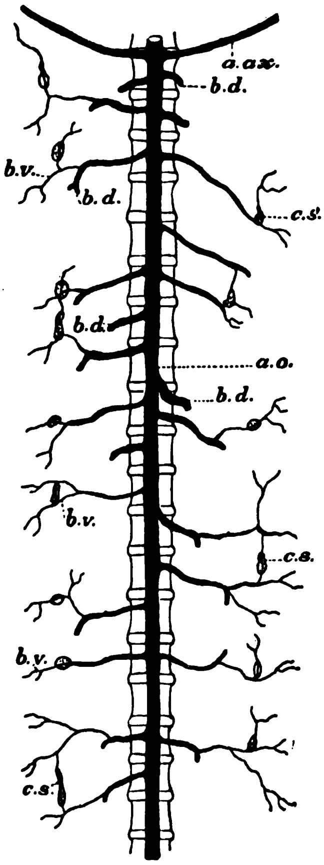

FIG. 371.—DIAGRAM OF THE SUPRARENAL ORGAN OF *Torpedo marmorata*. (After E. Grynfeldt.)

a.o, anterior part of the aorta and its branches; *a.ax*, axillary (subclavian) artery; *b.d*, dorsal, and *v.d*, ventral branches; *c.s*, suprarenal bodies.

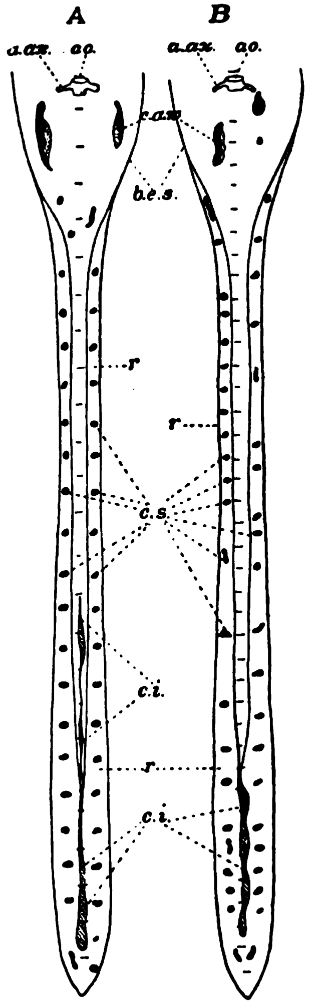

FIG. 372.—INTERRENAL AND SUPRARENAL ORGANS OF SQUALIDÆ. A, *Mustelus lævis*; B, *Centrina vulpecula*. (After E. Grynfeldt.)

ao, aorta; *a.ax*, axillary (subclavian) artery; *b.e.s*, outer margin of cardinal sinus; *c.ax*, the so-called "axillary body"; *c.i*, interrenal bodies; *c.s*, suprarenal bodies; *r*, kidney.

most numerous along its anterior portion, projecting into the lumen of the vessel so as only to be covered by its lining epithelium. Their connection with the sympathetic cannot, at any rate in most cases, be traced in the adult. The interrenals are of varied size and of a whitish or yellowish colour: they occur, enclosed in fibrous capsules, sometimes on the dorsal and sometimes on the ventral surface of the kidney, usually at its middle or posterior third, more or less embedded in its substance. They are usually paired, but rarely symmetrical on either side.

Amongst **Ganoids**, the suprarenals of Sturgeons are situated on the median side of the cardinal veins and on the revehent veins of the mesonephros: like the interrenals, they show many points of similarity to the corresponding organs in Teleosts.

Amongst **Dipnoans**, the suprarenals of Protopterus are closely related to the intercostal arteries all along the trunk-region, and have a paired and segmental arrangement. On the anterior part of the cardinal and postcaval vein chromaffin cells also occur.

In **Amphibians**, the interrenal and suprarenal organs become united to form a compound adrenal body. In the Myctodera, the main mass of the adrenal lies on the inner border of the kidney, from which it is plainly distinguishable by its yellow colour. It forms a band consisting of irregular lobes extending straight backwards all along the mesonephros, being most strongly developed at the middle part of the latter. Here, again, it is intimately related as regards position with the revehent renal veins, and often also with the postcaval and cardinal. In Anurans, the adrenal is usually situated on the ventral side of the kidney, and more or less towards its outer border, but reaching to its posterior end, and appearing like an irregular, yellow streak, the lobules of which follow closely the course of the revehent renal veins, around which they form a branched network: frequently certain of the lobules come into relation with the ventral wall of the postcaval.

In the **Amniota**, the restriction of the adrenals to more definite and localised regions is carried considerably further than in the Amphibia. They consist of a more uniform and circumscribed mass on either side in which both interrenal and suprarenal substances are included.

In the Sauropsida, the adrenals are met with in the form of elongated yellow areas, with smooth or lobed borders, in the immediate neighbourhood of the gonads. In Mammals, at a certain period of development of which (especially in Man, Fig. 348, B) they are relatively voluminous, the adrenals are situated near the kidneys, and the name of the organ is due to this fact. As in all other Vertebrates, these structures are closely related as regards position to the great vascular trunks of the body-cavity.

Although the two components are united in the adrenal of Amniota, in the Sauropsida the relation of the one to the other is not of the regular and characteristic kind seen in Mammals, but there seems to be an irregular mingling of both elements. In Mammals, on the other hand, as already mentioned, the interrenal forms the cortical substance enclosing the suprarenal portion or medulla, with its chromaffin tissue,[1] and the whole organ is richly supplied with pigment, lymph-vessels, and blood-vessels, although it possesses no portal system, as in Amphibia and Sauropsida. As regards form, there is considerable variation in the Mammalian adrenals; they may be compact and smooth, or more or less lobed, and are usually asymmetrical in position.

Physiological experiments on the adrenals indicate that they are of great functional importance, and the two chief theories with regard to them are briefly as follows. The medullary portion is said to be a gland with "internal secretion," and to give off into the blood a substance (*adrenalin*) which reacts on the muscular contraction of the heart and blood-vessels, and increases the blood-pressure. On the other hand, there is some evidence that the cortex takes part in the manufacture of a substance which is passed directly or indirectly into the blood-stream, and which destroys the useless or harmful products of destructive metabolism. Future researches must show whether and to what extent the theory of "internal secretion" or of "auto-intoxication" is universally applicable.

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[1] So-called "accessory suprarenals," consisting of nests of chromaffin cells, are found in all Vertebrates in relation with the sympathetic system and blood-vessels.

APPENDIX

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